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The Upper Cretaceous ammonite *Vascoceras* Choffat, 1898 in north-eastern Nigeria

P.M.P. ZABORSKI

Department of Geology and Mining, University of Jos, P.M.B. 2084, Jos, Nigeria

CONTENTS

Synopsis. Large collections of ammonites that have been referred at one time or another to *Vascoceras* Choffat, can be made under tight stratigraphical control in north-eastern Nigeria. The following forms are present, in order of stratigraphical appearance: *Paravascoceras cauvini* (Chudeau); *Vascoceras woodsi* sp. nov.; *V. bullatum* Schneegans, *V. globosum costatum* (Reyment), *V. globosum globosum* (Reyment) and *Pseudovascoceras nigeriense* (Woods); *V. globosum proprium* (Reyment); *V. obscurum* Barber; and *V. harttii* (Hyatt). Only the last three occur in the Lower Turonian; the remainder are restricted to the Upper Cenomanian, the earliest appearing above the level of the European *Metoicoceras geslinianum* Zone.

Paravascoceras Furon (type species *Vascoceras cauvini* Chudeau) is retained as a separate genus for forms derived from *Nigericeras* Schneegans. *Pseudovascoceras* gen. nov. (type species *Vascoceras nigeriense* Woods) is proposed for ribbed and multituberculated forms thought to have arisen from *Cunningtoniceras* Collignon. *Paravascoceras* and *Pseudovascoceras* are most properly referred to the subfamily Acanthoceratinae since they have an origin separate from that of *Vascoceras*.

Several of the taxa present show a high degree of individual variation. Palaeoecological factors played an important role in their geographical distribution and probably also in their potential for polymorphism. Separate lineages converged on a '*Vascoceras* morphology' in north-eastern Nigeria as a response to the particular environmental conditions prevailing there during Late Cenomanian and Early Turonian times.

INTRODUCTION

In Tethyan regions ammonites referred to the genus *Vascoceras* Choffat, 1898, are often present in large numbers in the Upper Cenomanian and Lower Turonian. The upper Benue Trough area in north-eastern Nigeria is a classic region for such faunas. Its ammonites have been described by Woods (1911), Reyment (1954*b*), Barber (1957, 1960), Meister (1989), Zaborski (1990*a*, 1993, 1995) and Courville (1992). Species of *Vascoceras* have been widely employed in biostratigraphical analysis in Nigeria but the taxonomic treatment applied to them has varied widely from author to author. The north-eastern Nigerian faunas are of particular interest since large collections can be made under

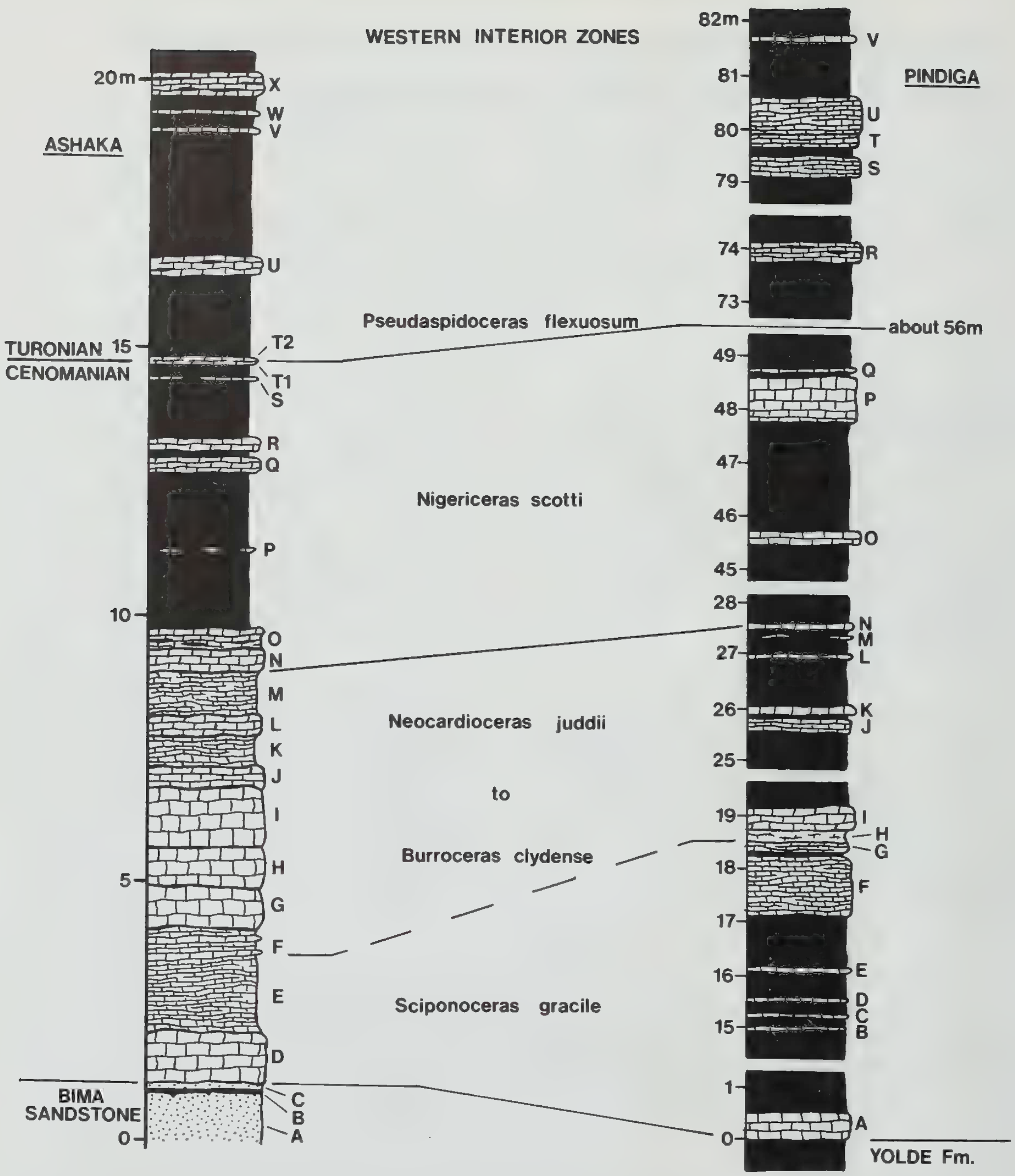


Fig. 1 Stratigraphical sections through the limestone-bearing parts of the Pindiga Formation at Ashaka and Pindiga with letter codes identifying limestone units mentioned in the text. Approximate biostratigraphical correlations with the ammonite biozones of the western interior of the United States (after Cobban *et al.* 1989, Hancock 1991) are also indicated.

tight stratigraphical control, especially at Ashaka quarry. Furthermore, dissection of adults is frequently successful in recovering well-preserved inner whorls which in some cases are invaluable for identification purposes, as well as for analysing ontogenetic development. These attributes have allowed a revised taxonomy to be presented here for the Nigerian faunas.

The family Vascoceratidae as a whole has been discussed by Spath (1925), Furon (1935), Schneegans (1943), Reyment (1954*b*, 1955, 1956), Barber (1957), Wiedmann (1960), Cooper (1978) and Wright & Kennedy (1981).

From the time of its proposal it has been recognized that the genus *Nigericeras* Schneegans, 1943 is morphologically intermediate between the subfamilies Acanthoceratinae and Vascoceratinae. More recently, a number of additional genera of intermediate character have been decribed, a notable feature being the combination of a vascoceratine-type suture pattern with an acanthoceratine-type ornament. Such intermediates include *Microdiphasoceras* Cobban, Hook & Kennedy (1989: 53), *Rubroceras* Cobban, Hook & Kennedy (1989: 54), *Fikaites* Zaborski (1993: 362) and *Pseudovascoceras*, described herein. It is believed here that the family Vascoceratidae is polyphyletic, including homeomorphic derivatives of various acanthoceratine genera. In Nigeria at least the same is true of forms previously referred to the genus *Vascoceras*.

SYSTEMATIC DESCRIPTIONS

Repositories. Unless otherwise stated all the specimens referred to below are housed in the Department of Palaeontology, The Natural History Museum, London, their register numbers being prefixed with the letter C. In addition to those specifically listed, large numbers of *Paravascoceras cauvini*, *Vascoceras woodsi*, *V. bullatum*, *V. globosum costatum*, *V. globosum globosum* and *Pseudovascoceras nigeriense* have also been studied.

Provenance of material. The ammonite-bearing horizons at the two main localities in north-eastern Nigeria, Ashaka and Pindiga, are shown in Fig. 1. A fuller description of these sections and lists of their ammonite faunas were given by Zaborski (1995). The Ashaka section has also been described by Wozny & Kogbe (1983), Popoff *et al.* (1986), Meister (1989) and Courville (1992). The Pindiga section has been described by Barber (1957), Carter *et al.* (1963), Wozny & Kogbe (1983) and Popoff *et al.* (1986). The whereabouts of other ammonite localities mentioned in the text were shown by Zaborski (1990*a*: fig. 1).

Dimensions (in mm). D, diameter; Wb, whorl breadth; Wh, whorl height; U, umbilical diameter. Figures in parentheses are dimensions as a percentage of the total diameter.

Superfamily **ACANTHOCERATACEAE** Grossouvre, 1894
Family **ACANTHOCERATIDAE** Grossouvre, 1894
Subfamily **ACANTHOCERATINAE** Grossouvre, 1894
Genus ***PARAVASCOCERAS*** Furon, 1935

(=*Paracanthoceras* Furon, 1935; *Pachyvascoceras* Furon, 1935; *Broggiiceras* Benavides-Cáceres, 1956)

TYPE SPECIES. *Vascoceras cauvini* Chudeau, 1909; by the subsequent designation of Reyment, 1955.

REMARKS. Furon (1935: 60) proposed *Paravascoceras* as a subgenus of *Vascoceras* and it has subsequently been treated as such by, for example, Schneegans (1943), Cooper (1978), Howarth (1985) and Meister *et al.* (1992). Others, for example Reyment (1955), Barber (1957), Wright (1957), Freund & Raab (1969), Schöbel (1975) and Meister (1989), have regarded it as a distinct genus while recently it has been widely listed as a synonym of *Vascoceras* (see, for example, Berthou *et al.* 1985, Kennedy *et al.* 1987, Luger & Gröschke 1989, Cobban *et al.* 1989).

Furon's original diagnosis of *Paravascoceras* specified non-globular forms characterized by a simple suture pattern which was said to distinguish it from *Paracanthoceras* Furon (1935: 59) (type species, by monotypy, *Vascoceras (Paracanthoceras) chevalieri* Furon, 1935). Both these forms show strong ventral ribbing in their later growth stages. Furon included *V. (P.) cauvini*, *V. (P.) cauvini* var. *semiglabra* Furon (1935) and *V. (P.) chudeaui* Furon (1935) in *Paravascoceras*. The last two are here regarded as synonyms of *P. cauvini*. Schneegans (1943: 127–128) showed that sutural differences between *Paravascoceras* and *Paracanthoceras* were insignificant and demonstrated the latter to be a synonym of the former. Indeed, *V. (Paracanthoceras) chevalieri* itself is a synonym of *Paravascoceras cauvini*. Schneegans gave a revised diagnosis of *Paravascoceras* stressing its vascoceratid suture pattern, ovoid to globular whorl section, lack of tubercles and possession of simple ventral ribs or folds in the adult stages. The absence of umbilical tubercles has since been cited as a chief distinguishing feature of *Paravascoceras* (see, for example, Freund & Raab 1969, Schöbel 1975, Meister 1989, Meister *et al.* 1992). Berthou *et al.* (1985), however, regarded the presence or absence of umbilical tubercles in *Vascoceras* as an inadequate basis for generic and subgeneric diagnosis, a conclusion accepted by Kennedy *et al.* (1987) and Cobban *et al.* (1989). This view is supported here. There is great inconsistency in this feature even within individual species of *Vascoceras*. Meister *et al.* (1992: 70; see also below) further showed that *P. cauvini* may itself show umbilical tubercles at certain growth stages.

As pointed out by Schneegans (1943: 127), the juvenile stages are often of greater value in taxonomic subdivision of *Vascoceras* than the often highly variable middle and adult whorls. Morphological and stratigraphical evidence from north-eastern Nigeria indicates that *Paravascoceras* was derived from *Nigericeras* (type species *Nigericeras gignouxi* Schneegans, 1943: 119, pl. 5, figs 10–15 = *N. gadeni* (Chudeau); by the subsequent designation of Reyment 1955: 62), an origin separate from that of *Vascoceras* (see below). In recognition of this probability *Paravascoceras* is here treated as a distinct genus. In view of its ornament and suture pattern *Nigericeras* should be included in the subfamily Acanthoceratinae (see also Kennedy *et al.* 1989, Cobban *et al.* 1989, Kennedy & Wright in press). *Paravascoceras*, therefore, cannot be maintained within the Vascoceratidae but should be transferred to the Acanthoceratinae also.

There remain problems in providing a reliable and unambiguous morphological diagnosis of *Paravascoceras*. Its members are generally compressed, moderately involute, without umbilical tubercles and with strong regular ribbing on the outer flanks and venter in the later growth stages. The last two features are not, however, consistent while certain rather depressed forms may belong in the genus.

Vascoceras (Pachyvascoceras) Furon (1935: 58) (type species *Vascoceras (Pachyvascoceras) crassus* Furon 1935: 58, pl. 3, figs 2a, b; by the subsequent designation of Reyment 1954*b*: 257) was proposed on the basis of its globular shape, deep narrow umbilicus and lack of adult ornament. None of these morphological features is sufficient to distinguish *Pachyvascoceras* from *Vascoceras*. Whorl breadth is often particularly variable within individual species of that genus. The phylogenetic affinities of *V. (P.) crassum*, however, may lie with *Paravascoceras* rather than *Vascoceras*. Meister *et al.* (1992) described topotype material which they regarded as variants of *Paravascoceras cauvini* with which they are transitional (see also Schneegans 1943). *Pachyvascoceras* is accordingly treated here as a probable synonym of *Paravascoceras* (see also below under *Vascoceras bullatum* and *V. globosum*).

The genus *Broggiiceras* Benavides-Cáceres (1956: 469–470) was proposed for the Peruvian forms *B. olssoni* Benavides-Cáceres (1956: 471, pl. 55, figs 1–4), the type species, and *B. humboldti* Benavides-Cáceres (1956: 471, pl. 56, figs 3–6). These forms have smooth inner whorls and an adult ornament of strong ventral ribs matching that in *P. cauvini*. *B. olssoni* has whorls a little broader than high. While the opposite condition may prevail on the body-chamber of *B. humboldti*, the two are probably synonyms. In the absence of any significant recorded differences from *Paravascoceras*, *Broggiiceras* is best regarded as a synonym. Schöbel (1975) and Meister *et al.* (1992), indeed, considered both *B. olssoni* and *B. humboldti* as synonyms of *P. cauvini*.

Figs 2–8 *Paravascoceras cauvini* (Chudeau). Figs 2–4, Pindiga Formation, unit K, Ashaka. Fig. 2a, b, C.93336, ×1. Fig. 3, C.93337, ×1. Fig. 4a, b, C.93338, ×1. Fig. 5a, b, Pindiga Formation, unit F, Ashaka. C.93556a, ×1. Figs 6, 7, Pindiga Formation, unit O, Ashaka. Fig. 6a, b, C.93518, ×1. Fig.7 a, b, C.93313, ×1. Fig. 8a, b, Pindiga Formation, unit H, Pindiga. C.93540, ×1.
Figs 9–11 *Vascoceras woodsi* sp. nov. Figs 9, 10, Pindiga Formation, Deba Habe. Fig. 9a, b, paratype, C.93596a, ×2. Fig. 10a, b, paratype, C.93596c, ×2. Fig. 11a, b, Pindiga Formation, unit M, Pindiga. Paratype, C.91264, ×1.

Paravascoceras cauvini (Chudeau, 1909) Figs 2–8

1909 *Vascoceras cauvini* Chudeau: 68, pls 1, 2; pl. 3, figs 1, 2.
1921 *Thomasites cauvini* (Chudeau) Chudeau: 463, fig. 1.
1933 *Vascoceras cauvini* Chudeau; Furon: 268, pl. 9, fig. 9.
1935 *Vascoceras (Paracanthoceras) Chevalieri* Furon: 59, pl. 4, figs 1a, b.
1935 *Vascoceras (Paravascoceras) Cauvini* Chudeau Furon: 60, pl. 5, figs 1a, b.
1935 *Vascoceras (Paravascoceras) Chudeaui* Furon: 61, pl. 4, fig. 2.
1935 *Vascoceras (Paravascoceras) Cauvini* Chudeau nov. var. *semiglabra* Furon: 61, pl. 4, fig. 3.
1943 *Paravascoceras cauvini* (Chudeau); Schneegans: 128, pl. 4, fig. 2.
1943 *Paravascoceras cauvini* var. *evoluta* Schneegans: 130, pl. 8, fig. 2.
1943 *Paravascoceras cauvini* var. *inflata* Schneegans: 131.
1943 *Paravascoceras chevalieri* Furon Schneegans: 132, pl. 4, fig. 7.
1957 *Vascoceras bulbosum* (Reyment) Barber: 19, pl. 6, figs 6, 8; pl. 27, figs 1–6.
1957 *Vascoceras depressum* Barber: 19, pl. 6, fig. 5; pl. 27, figs 7–9.
?1957 *Paravascoceras* aff. *cauvini* (Chudeau); Barber: 37, pl. 14, figs 2, 3; pl. 32, figs 8, 9.
?1965 *Paravascoceras* aff. *cauvini* (Chudeau); Collignon: 183.
1969 *Paravascoceras cauvini* (Chudeau); Freund & Raab: 20, pl. 3, figs 1–3; text-figs 5a, b.
1969 *Paravascoceras tavense* (Faraud) Freund & Raab: 23, pl. 2, fig. 9, text-figs 5e–g.
1975 *Paravascoceras cauvini* (Chudeau); Schöbel: 119, pl. 4, fig. 3; pl. 5, figs 1–4.
?1981 *Paravascoceras cauvini* (Chudeau); Collignon & Roman (*in* Amard, Collignon & Roman): 51, pl. 3, fig. 9.
?1981 *Paravascoceras chevalieri* (Furon); Collignon & Roman (*in* Amard, Collignon & Roman): 52, pl. 6, figs 1, 2.
?1981 *Nigericeras barcoicense* (Choffat) Collignon & Roman (*in* Amard, Collignon & Roman): 54, pl. 4, figs 16a, b.
1989 *Vascoceras cauvini* Chudeau; Luger & Gröschke: 374, pl. 40, figs 3, 6, 8, 9; pl. 41, figs 1–4; pl. 42, fig. 1; text-figs 6G, H, 8C.
1989 *Nigericeras gadeni* (Chudeau) *lamberti* Schneegans; Meister: 10, pl. 3, figs 1–3; text-fig. 6.
1989 *Nigericeras jacqueti* Schneegans; Meister: 11, pl. 2, figs 3, 4; pl. 4, fig. 1; text-fig. 7.
1989 *Paravascoceras* aff. *nigeriense*? (Woods) Meister: 16, pl. 5, fig. 3.
1990*a* *Vascoceras cauvini* Chudeau; Zaborski: figs 8, 12–15.
1990*a* *Vascoceras bulbosum* (Reyment); Zaborski: fig. 11.
1992 *Vascoceras (Paravascoceras) cauvini* (Chudeau); Meister, Alzouma, Lang & Mathey: 71, pl. 4, fig. 6; pl. 5, fig. 1, pl. 6, fig. 2.
1992 *Vascoceras (Paravascoceras) cauvini* forme *lisse* Meister, Alzouma, Lang & Mathey: 72, pl. 5, fig. 2; pl. 6, figs 1, 3.
1992 *Vascoceras (Paravascoceras) cauvini* forme *comprimée* Meister, Alzouma, Lang & Mathey: 72, pl. 5, fig. 3; pl. 6, fig. 4.
1992 *Vascoceras* gr. *cauvini* Chudeau; Courville: pl. 4, figs 1–3.

MATERIAL AND OCCURRENCE. Thirty-six specimens, C.91304, Pindiga Formation, unit E, Ashaka; C.93556a, b, C.93557-9, C.93932, Pindiga Formation, unit F, Ashaka; C.93336-8, Pindiga Formation, unit K, Ashaka; C.91271-4, C.93304, C.93313, C.93517-8, Pindiga Formation, unit O, Ashaka; C.91278-84, C.93540-2, C.93933, Pindiga Formation, unit H, Pindiga; C.91285-9, C.93539, Pindiga Formation, unit J, Pindiga; C.91312, Pindiga Formation, unit N, Pindiga. The species has a known stratigraphical range from unit E (upper half) to unit O at Ashaka and from unit G to unit N at Pindiga.

DIMENSIONS. See Fig. 12.

REMARKS. In north-eastern Nigeria *Paravascoceras cauvini* includes forms showing whorls slightly to distinctly higher than broad, with rounded to slightly flattened venters and an umbilicus representing 16–29% of the total diameter. The species has a relatively long stratigraphical range here but successive assemblages show some variation.

Material from unit F at Ashaka reaches a maximum diameter of some 100 mm. The adult whorls are smooth or with weak, irregular, crease-like ventral ribbing. The inner whorls, however, may show alternating long and short ribs (Fig. 5). The long ribs arise at umbilical tubercles. All ribs bear vague ventrolateral swellings but there are no siphonal tubercles. Umbilical tubercles or bulges may persist into the middle growth stages. This umbilical ornament is especially pronounced in certain specimens collected from the equivalent horizon (unit H) at Pindiga.

Material from unit K at Ashaka is the oldest found to show the strong ventral adult ribbing which characterizes the species (Fig. 3; Meister 1989: pl. 3, fig. 1).

Material from unit O can be regarded as fully typical of *P. cauvini*. The inner whorls (Fig. 6) are completely smooth. This is usually the case with the middle growth stages also but rare individuals show bullate to clavate umbilical tubercles. Even less frequently there are broad, low, ventrolateral swellings but such features disappear by a diameter of 45 mm. Ventral ribbing is commonly displayed in the later growth stages (see Zaborski 1990*a*: fig. 14) but this ornament appears at a diameter varying from 60 mm to over 100 mm and is sometimes lacking altogether. Adults reach a maximum diameter of over 160 mm.

In general whorl proportions *P. cauvini* is a very close match for *Nigericeras gadeni* (Chudeau). The middle and adult whorls of the two may be difficult to distinguish unless sutures are visible; *N. gadeni* has square saddles, a narrow L and a distinctly bifid E/L, *P. cauvini* has more rounded and evenly frilled saddles. The material from Ashaka referred to *Nigericeras* by Meister (1989) in fact belongs in *P. cauvini*. The early whorls of *N. gadeni* are distinct, showing a typically acanthoceratine ornament with long and short ribs and seven rows of tubercles (see Schneegans 1943, Zaborski 1990*a*, Meister *et al.* 1992). Vestiges of a similar ornament, but without siphonal tubercles however, occur in early *P. cauvini* from unit F at Ashaka. The middle whorls of specimens from unit H at Pindiga sometimes show the strong bulge-like umbilical tubercles that are common at the same growth stage in *N. gadeni*. Meister *et al.* (1992: 70) and Courville (1992: 415) have also drawn attention to similarities between the juvenile ornament and in some cases suture pattern of *P. cauvini* and *Nigericeras*.

Nigericeras gadeni characterizes the basal ammonite-bearing beds in north-eastern Nigeria, occurring in unit D at Ashaka and unit A at Pindiga. It therefore predates *P. cauvini*. It is probable that *P. cauvini* is derived from *N. gadeni* by a progressive

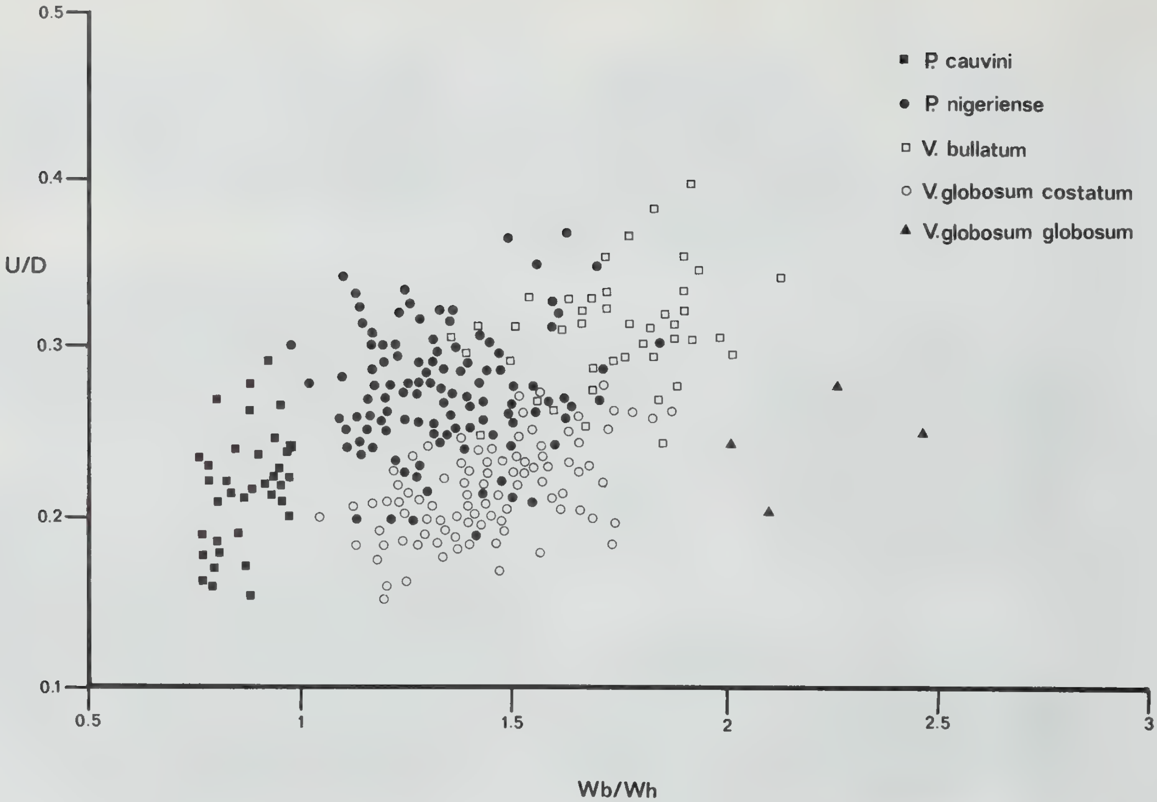


Fig. 12 Shell proportions in *Paravascoceras cauvini* (Chudeau), *Pseudovascoceras nigeriense* (Woods), *Vascoceras bullatum* Schneegans, *V. globosum costatum* (Reyment) and *V. globosum globosum* (Reyment) from unit O at Ashaka. These individuals are the product of collecting carried out over the course of two hours specifically for the purpose of comparing dimensions. This figure also gives a good indication of the relative abundances of the taxa concerned.

loss of juvenile ornamentation (peramorphosis), simplification of suture pattern and development of adult ribbing. Forms from unit F at Ashaka and unit H at Pindiga are transitional in nature.

Schneegans (1943: 119–125) proposed three additional species of *Nigericeras*, *N. gignouxi*, *N. lamberti* and *N. jacqueti* which show an increasingly weaker ornament but which all display the typically acanthoceratine suture pattern of the genus. It may be noted that in north-eastern Nigeria there is a variation in the strength of ornament of *Nigericeras* collected from place to place. Individuals from Teli and from north-east of the Biu Plateau (see Zaborski 1990*a*: figs 4, 5) have a weak juvenile ornament while those from the Hinna region and from between Kanawa and Wajari (see Zaborski 1990*a*: figs 6, 7) have stronger ornament. There is, however, no available evidence of this variation having a stratigraphical significance. In Niger, forms of *N. jacqueti* type occur alongside typical *N. gadeni* (Meister *et al.* 1992).

In north-eastern Nigeria *N. gadeni* occurs in the equivalent of the Geslinianum Zone in north-west Europe and the Gracile Zone in the western interior of the United States (Zaborski 1990*a*). *P. cauvini* ranges through the probable equivalents of the Juddii Zone in north-west Europe and the Clydense to Scotti zones in the western interior (see below). Lewy *et al.* (1984) described *P. cauvini* in association with *Metoicoceras geslinianum* (d'Orbigny) in Israel. Their material, however, shows broad flank ribbing and umbilical bulges (Lewy *et al.* 1984: fig. 4I) in its middle whorls, features more typical of *Nigericeras* from which it appears to be transitional. Its suture is unknown.

Cooper (1979) and Kennedy & Wright (in press) proposed an origin for *Nigericeras* within *Pseudocalycoceras* Thomel, 1969. The early whorls in *Nigericeras*, however, also resemble the dwarf *Protacanthoceras bunburianum* (Sharpe) (see Wright & Kennedy 1980: 91, figs 29–33, 41–43, 48; 1987: 215, pl. 55, figs 10–16; text-figs 83B, C, 84D–H), a lowest Upper Cenomanian Guerangeri Zone species. *Nigericeras* may be a peramorphic derivative.

The small Nigerian specimens from low in the Pindiga section referred to *Vascoceras bulbosum* (Reyment) and *V. depressum* sp. nov. by Barber (1957) are here regarded as *P. cauvini* as is the material from Ashaka included in *Nigericeras* by Meister (1989).

The *P. cauvini* from Nigeria are compressed forms which fall into a distinct morphological group within the ammonite fauna from unit O at Ashaka (Fig. 12). Individuals from Niger, however, develop a broader whorl section (see Meister *et al.* 1992: pl. 6, fig. 2). These specimens seem to be of the same age as those from unit O at Ashaka. The latter are associated with very large numbers of more inflated ammonites referrable to *Vascoceras globosum costatum*, *V. bullatum* and *Pseudovascoceras nigeriense*. These three forms are of markedly less importance in Niger, if they are present at all. Their possible absence may have allowed populations of *P. cauvini* in Niger to develop a greater range of morphotypes due to lack of competition. Meister *et al.* (1992: 72–76) described a number of additional forms from Niger as *Vascoceras (Paravascoceras) cauvini* forme *crassum* (Furon) and *V. (P.) cauvini* forme de transition entre forme *crassum* et *V. (P.) proprium* (Reyment) . They are further discussed below under *Vascoceras globosum*.

Also of interest in regard to their general whorl proportions are *Paravascoceras rumeaui* Collignon (1957: 122, pl. 16, fig. 2; Freund & Raab 1969: 21, pl. 3, figs 4, 5; text-figs 6c, d; Luger & Gröschke 1989: 380, pl. 41, figs 5, 6; pl. 42, figs 3, 4; text-fig. 8D) from Algeria, Egypt and Israel and *Vascoceras costellatum* Collignon & Roman (*in* Amard *et al.* 1981: 51, pl. 2, figs 6a, b) from Algeria. These species have adult ventral ribbing like that in *P. cauvini* but are more inflated. They may, like the Niger forms, be regional variants of *P. cauvini*. Luger & Gröschke (1989: 375–376) discussed the question of whorl breadth in *P. cauvini* but, unlike Schöbel (1975), regarded *P. rumeaui* as distinct from *P. cauvini*. They further separated individuals with depressed whorls but which were otherwise similar to *P. cauvini* as *Vascoceras* cf. *cauvini* (Luger & Gröschke 1989: 376, pl. 42, fig. 2; pl. 43, fig. 3; text-figs 6F, 8B).

The *P. cauvini* of Collignon & Roman (*in* Amard *et al.* 1981: 51, pl. 3, fig. 9) have whorls only a little broader than high and probably belong here. Their *Paravascoceras chevalieri* (Furon) (Collignon & Roman *in* Amard *et al.* 1981: 52, pl. 6, figs 1, 2) and *Nigericeras barcoicense* (Choffat) (Collignon & Roman *in* Amard *et al.* 1981: 54, pl. 4, figs 16a, b) are similar to and may be conspecific with *P. cauvini*. The *Paravascoceras* aff. *chevalieri* of Reyment (1955: 63, pl. 14, figs 1a, b), however, shows three rows of tubercles upon the ventral ribs and more closely resembles early *Thomasites gongilensis* from unit O at Ashaka (see Figs 41–44).

The *Vascoceras (Paravascoceras)* cf. *cauvini* from Angola described by Cooper (1978: 130, figs 6C–H, 35–37) is a *Nigericeras*.

Berthou *et al.* (1985: 72) speculated that *Vascoceras barcoicense* Choffat (1898: 67, pl. 17, fig. 1; pl. 22, fig. 5; Berthou *et al.* 1985: 70, pl. 4, figs 1–3) might turn out to be a senior synonym of *P. cauvini*. The strong adult ribbing of the latter species is, however, unknown in *V. barcoicense*. Whorl proportions in the two are similar but nothing is known of the early growth stages in *V. barcoicense*. The species may belong in *Paravascoceras* or alternatively it may be an involute, weakly ornamented variant of *Vascoceras gamai* Choffat, according to Berthou *et al.* (1985: 71).

V. barcoicense exile Cobban, Hook & Kennedy (1989: 47, figs 47, 87Q-S, 89M-GG) from New Mexico resembles *P. cauvini* in whorl proportions but is more involute. Specimens from low in the Pindiga section may be similar in this respect (Fig. 8) but *V. barcoicense exile* has a different juvenile ornament of rather strong ventral ribs. The *V. (V.) cauvini* of Kennedy *et al.* (1989: 82, figs 9G, 20C-G) from Texas are similar to and probably conspecific with *V. barcoicense exile*.

Further involute compressed forms are the *Nigericeras jacqueti involutum* Meister, Alzouma, Lang & Mathey (1992: 68, pl. 4, figs 3–5; text-fig. 14) from Niger. Again, these show similarities with *P. cauvini* from unit H at Pindiga but are consistently more involute. Their suture pattern (Meister *et al.* 1992: fig. 14) is incompletely known but seems to be intermediate between that of *Nigericeras* and *Paravascoceras*. Meister *et al.* (1992) regarded *N. jacqueti involutum* as an offshoot of *N. gadeni* derived through *N. jacqueti jacqueti*. It may be the product of a local lineage independent of that giving rise to *P. cauvini*.

Genus ***PSEUDOVASCOCERAS*** gen. nov.

TYPE SPECIES. *Vascoceras nigeriense* Woods, 1911.

DIAGNOSIS. Moderately evolute to moderately involute, moderately compressed to moderately depressed ammonites. Whorls rounded to subpentagonal. Ornament of umbilical, inner and outer ventrolateral and siphonal tubercles which may be borne upon transverse to concave ribs of varying strength. Additional ventral ribs frequently present. Ornamental elements of highly variable persistence during ontogeny, sometimes extending onto the body-chamber, in other cases confined to the earliest growth stages. Suture line simple with evenly frilled elements; saddles often elongate and rectangular in outline, lateral lobe fairly broad.

REMARKS. Of all the ammonites from north-eastern Nigeria showing 'vascoceratid' suture patterns it is the multituberculated forms which have proved most problemmatical and which have received the most varied taxonomic treatment. This is not surprising given the huge range of morphotypes that are represented within assemblages from the same stratigraphical horizon, at Ashaka unit O. In fact three multituberculated genera are present therein, end members of which are not always easy to differentiate. Forms attributable to *Rubroceras* Cobban, Hook & Kennedy occur as rarities (Zaborski 1993); a larger number of individuals belong in *Fikaites* Zaborski (1993); but the greatest number are here referred to *Pseudovascoceras nigeriense* (Woods).

In his treatment of this last group Barber (1957) assigned them to three genera, *Vascoceras*, *Nigericeras* and *Paramammites* Furon, and no less than seven species. The last two generic determinations can easily be disposed of. The type species of *Paramammites* (by the subsequent designation of Reyment 1954*b*: 225), *Vascoceras polymorphum* Pervinquière (1907: 336, pl. 21, figs 2, 6; text-fig. 126) (see also Renz 1982: 84–85; Chancellor *et al*, in press) has a juvenile ornament of varying strength, often with large spinose tubercles, but always lacks siphonal tubercles. The present material has nothing to do with *Paramammites*. Forms with strong adult costae, interrupted ventrally, have often been referred to this genus without knowledge of their ontogenetic development (see also Cobban *et al.* 1989: 51; Zaborski 1990*b*: 574–575) thus creating a rather confused situation. *Nigericeras* resembles the present material in only one real respect, the presence of seven rows of tubercles. In detail its ornament is more regular and in all genuine members of the genus it is confined to the early whorls (see Schneegans 1943). The suture in *Nigericeras*, although simple, is of a distinctly acanthoceratine pattern, unlike that in the present material and other forms mentioned below also previously referred to *Nigericeras*. Nor can the present material be referred to *Vascoceras*. Its ornament is unlike than in any known species of the genus and quite distinct from that in the type species *V. gamai*.

Cobban *et al.* (1989: 51) pointed out that Barber's (1957) *Paramammites* needed a new generic name. They suggested that these forms were in part ribbed and tuberculated derivatives of *Vascoceras*. The genus *Pseudovascoceras* is here proposed to include this material, the name alluding to the homeomorphy between smooth members of the type species and true *Vascoceras*. The origin of the genus, however, is thought to lie in an earlier acanthoceratine genus, probably *Cunningtoniceras* Collignon, 1937 as detailed below.

Nigericeras scotti Cobban (1971: 18, pl. 9, figs 1–4; pl. 18, figs 1–9; text-figs 15–19) from the terminal Cenomanian of the United States western interior may be a *Pseudovascoceras*. It lacks the suture pattern typical of *Nigericeras* but resembles the more strongly ornamented examples of *P. nigeriense*.

The unnamed specimen from Turkestan figured by Kler (1909: pl. 8, figs 3a, b; text-fig. 6) may also be a *Pseudovascoceras*.

The English specimen (C.82287) from the high Cenomanian referred to *Nigericeras* cf. *gignouxi* Schneegans by Wright & Kennedy (1981: 85, pl. 15, figs 6a, b) is a fragment, the ornament and suture pattern of which cannot be made out clearly. It might be best referred to *Pseudovascoceras*. It occurs alongside *Thomasites gongilensis*. In Nigeria *Thomasites* occurs well above the stratigraphical level of *Nigericeras,* but its earliest members are coeval with *P. nigeriense*.

Pseudovascoceras nigeriense (Woods, 1911)

Figs 14–24, 36, 37

- ?1909 *Vascoceras cauvini* Chudeau: pl. 3, figs 4a, b (only).
- 1911 *Vascoceras nigeriense* Woods: 281, pl. 21, fig. 6; pl. 22, figs 2, 3.
- ?1943 *Vascoceras nigeriense* Woods; Schneegans: 133, pl. 4, fig. 1.
- ?1943 *Paravascoceras* cf. *barcoicense* (Choffat) Schneegans: 134, pl. 8, fig. 1.
- 1954*b* *Vascoceras nigeriense* Woods; Reyment: 256.
- ?1955 *Nigericeras ogojaense* Reyment: 62, pl. 13, fig. 6; pl. 14, fig. 3; text-fig. 28.
- 1957 *Vascoceras nigeriense* Woods; Barber: 15, pl. 4, fig. 2; pl. 26, figs 1, 2.
- 1957 *Nigericeras costatum* Barber: 29, pl. 10, figs 3, 4; pl. 11, fig. 3; pl. 30, figs 1–7.
- 1957 *Nigericeras glabrum* Barber: 29, pl. 10, figs 1, 2; pl. 30, fig. 8.
- 1957 *Nigericeras? intermedium* Barber: 31, pl. 11, figs 1, 2; pl. 30, figs 9, 10.
- 1957 *Paramammites tuberculatus* Barber: 31, pl. 12, fig. 1; pl. 13, fig. 2; pl. 31, figs 1–3, 9.
- 1957 *Paramammites raricostatus* Barber: 33, pl. 12, fig. 3; pl. 31, figs 4, 6, 7.
- 1957 *Paramammites inflatus* Barber: 33, pl. 12, fig. 2; pl. 13, fig. 1; pl. 31, figs 5, 8.
- ?1965 *Paramammites laffitei* Collignon: 186, pl. A, fig. 2.
- ?1965 *Paramammites subtuberculatus* Collignon: 187, pl. A, fig. 3.
- 1965 *Vascoceras nigeriense* Woods; Reyment: pl. 2, fig. 2.
- 1965 *Nigericeras costatum* Barber; Reyment: pl. 3, fig. 13.
- ?1965 *Nigericeras ogojaense* Reyment; Reyment: pl. 3, fig. 14.
- 1965 *Paramammites tuberculatus* Barber; Reyment: pl. 3, figs 15a, b.
- 1980 *Nigericeras costatum* Barber; Wright & Kennedy: figs 10a, b.
- 1989 *Paravascoceras nigeriense*? (Woods); Meister: 14, pl. 5, fig. 1; pl. 6, fig. 1; text-fig. 11.
- 1989 *Vascoceras costatum* (Barber) Meister: 23, pl. 10, figs 3, 5; pl. 11, figs 1, 2, 5; text-figs 16a–d.
- 1989 *Vascoceras costatum glabrum* (Barber) Meister: 23, pl. 9, figs 2, 4; pl. 10, fig. 4; text-figs 16e–g.
- 1989 *Vascoceras ellipticum* Barber; Meister: 28, pl. 12, figs 1, 3; text-fig. 18.
- 1989 *Paramammites subconciliatus* (Choffat) Meister: 30, pl. 12, figs 4, 5; pl. 13, figs 1–4; pl. 14, figs 1, 2; pl. 15, figs 1, 4; text-fig. 21.
- 1989 *Paramammites polymorphus* (Pervinquière); Meister: 36, pl. 14, figs 3, 4; text-fig. 24.
- 1990*a* *Vascoceras nigeriense* Woods; Zaborski: fig. 25.
- 1992 *Vascoceras* sp. gr. *costatum* (Barber) *sensu* Meister, 1989; Courville: pl. 5, fig. 3; pl. 6, figs 2, 3.

LECTOTYPE. Specimen B3237, Sedgwick Museum, Cambridge (see Woods 1911: pl. 22, figs 2, 3); from Kunini, north-eastern Nigeria (selected by Berthou, Chancellor & Lauverjat 1985: 69).

PRESENT MATERIAL AND OCCURRENCE. Sixty-one specimens, C.93305-8, C.93311, C.93315-21, C.93370-93, C.93494a–d, C.93495a–f, C.93496a–d, C.93497-507, Pindiga Formation, unit O, Ashaka.

DIMENSIONS. See Fig. 12.

REMARKS. *P. nigeriense* is generally a moderately evolute species having rather compressed to moderately depressed whorls with a rounded to subpentagonal outline. In overall shell proportions it overlaps with both *Vascoceras bullatum* and *V. globosum costatum*; smooth individuals are often especially difficult to distinguish from the last form. The adult diameter varies from about 85 to 120 mm when the body-chamber makes up two-thirds of the final whorl.

It is in its ornamentation that *P. nigeriense* shows its greatest variation, from almost entirely smooth to highly decorated end members. A variation series is shown in Figs 14–24, and there is also abundant figured material in the previous literature (see synonymy list). Dissection of numerous individuals, including those with smooth outer whorls, shows that siphonal tubercles are consistently developed but they may have already disappeared by a diameter of 10 mm. Outer ventrolateral tubercles are also commonly developed while inner ventrolateral and umbilical tubercles may or may not be present. One combination or another of tubercle rows may persist throughout the length of the septate whorls or disappear at any stage in ontogeny. Umbilical tubercles, when present, are the most persistent ornamental features and siphonal tubercles are the least, with the result that numerous individuals show six rows of tubercles in their middle growth stages. Strongly tuberculated forms may in addition display rectiradiate to concave ribs connecting the tubercles. The ribs may branch across the venter while additional ribs with inner and/or outer ventrolateral and siphonal tubercles may be intercalated. Ornamental strength is initiated very early in ontogeny. The ornament of the phragmocone may persist onto the adult body-chamber or this part of the shell may be smooth. Most frequently, however, there are irregularly developed ribs upon the flanks and the venter which vary from strong, broad fold-like structures to fine, dense crease-like features recalling those in adult *Vascoceras woodsi* and *V. bullatum*.

Suture patterns are of a simplified type but the saddles tend to be elongated, especially in strongly ornamented forms. The lateral lobe is fairly wide and often subdivided by a distinct median element.

Meister (1989) separated members of *P. nigeriense* from Ashaka into six taxa, *Paravascoceras nigeriense* (Woods), *Vascoceras ellipticum* Barber, *Paramammites* aff. gr *polymorphus* (Pervinquière), *P. subconciliatus* (Choffat), *Vascoceras costatum* (Barber) and *V. costatum glabrum* (Barber). Nevertheless, he showed how the ornamental variation between the last three could easily be interpreted in terms of

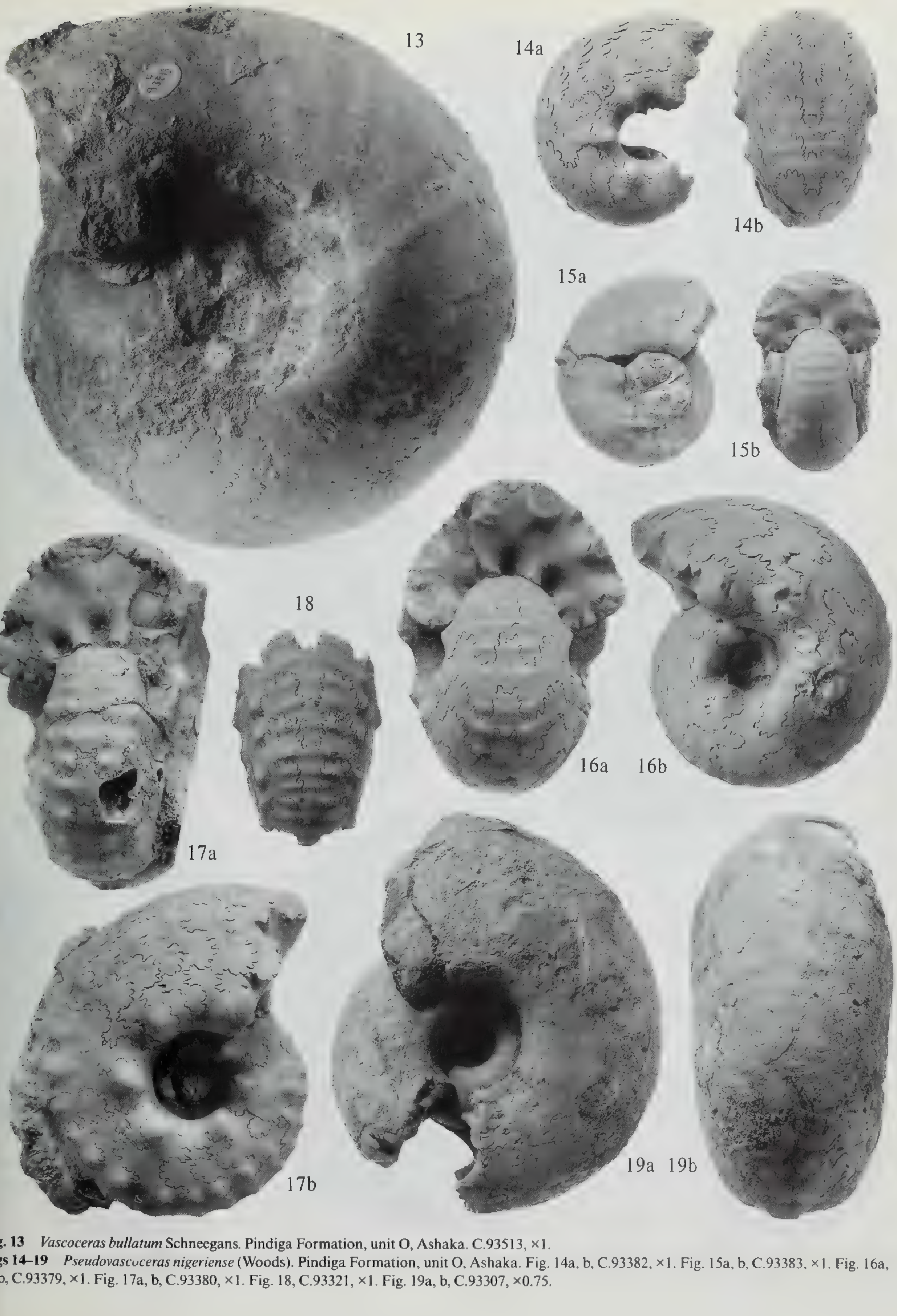
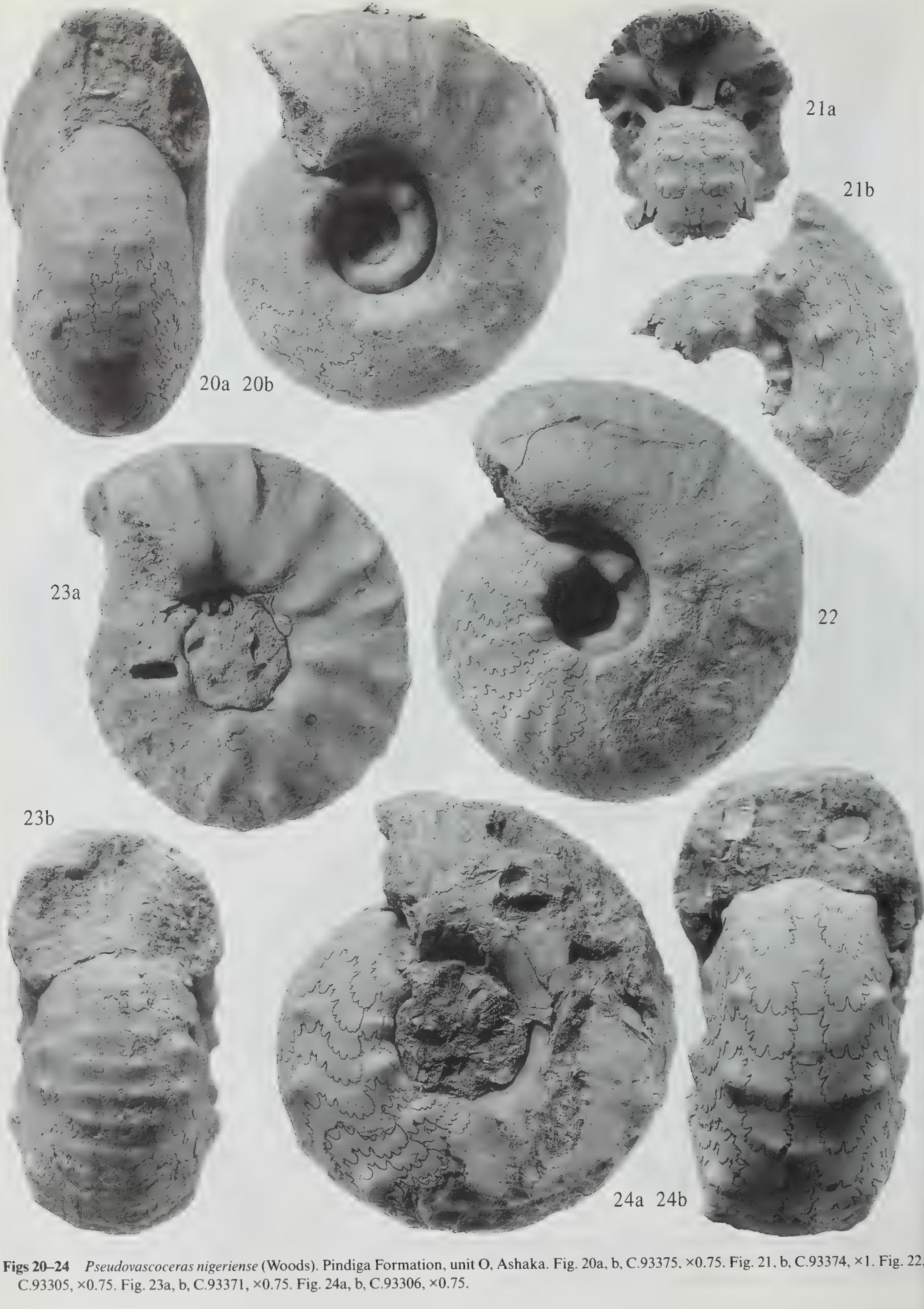


Fig. 13 *Vascoceras bullatum* Schneegans. Pindiga Formation, unit O, Ashaka. C.93513, ×1.
Figs 14–19 *Pseudovascoceras nigeriense* (Woods). Pindiga Formation, unit O, Ashaka. Fig. 14a, b, C.93382, ×1. Fig. 15a, b, C.93383, ×1. Fig. 16a, b, C.93379, ×1. Fig. 17a, b, C.93380, ×1. Fig. 18, C.93321, ×1. Fig. 19a, b, C.93307, ×0.75.



Figs 20–24 *Pseudovascoceras nigeriense* (Woods). Pindiga Formation, unit O, Ashaka. Fig. 20a, b, C.93375, ×0.75. Fig. 21, b, C.93374, ×1. Fig. 22, C.93305, ×0.75. Fig. 23a, b, C.93371, ×0.75. Fig. 24a, b, C.93306, ×0.75.

heterochronic ontogenies (Meister 1989: 34, 36, text-fig. 23). Concerned, however, that the faunas from unit O at Ashaka were condensed and might contain chronologically successive taxa, he refrained from placing them in synonymy. Unit O at Ashaka is the product of a 'slow' rate of sediment accumulation associated with a marine flooding phase. It contains the most diverse marine fauna found at Ashaka including numerous bivalves, gastropods and echinoids as well as a large number of ammonite species (see also Courville 1992: fig. 2). Encrustations of *Plicatula* occur throughout while many of the ammonites show oyster and serpulid overgrowths. There is, however, no significant phosphatization or reworking, and glauconite is rare or absent. There is no reason to believe that this unit represents any greater condensation than several other limestones at Ashaka and elsewhere in north-eastern Nigeria. Phosphatic matter, glauconite and reworked ammonites are common components in the limestone beds of the region, particularly in the upper parts of those interbedded with shales. It is the upper surface of unit O at Ashaka that marks the most significant break in sedimentation, but *P. nigeriense* is found throughout the unit below this level. Both Meister (1989) and Courville (1992) believed they could differentiate between faunas from different levels in unit O (their Niveau 21 and Niveau 22), though their reported successions differ. No significant stratigraphical variation in the nature of the ammonite faunas from this unit has been detected in the present work, apart from the restriction of strongly ornamented *Thomasites* to its upper surface. In the cases of the other ammonites present intraspecific variation is by far the most important factor. No morphometric or ornamental evidence has been obtained which allows objective taxonomic subdivision of *P. nigeriense*. There is a complete intergradation from smooth to strongly ornamented individuals while the latter vary considerably among themselves. In view of these factors all these morphotypes are regarded as conspecific, despite the great differences between end members. Courville (1992: 419–420) came to a similar conclusion and favoured the name *Vascoceras costatum* (Barber) which was used by Meister (1989) for individuals of intermediate ornamental strength. Priority, however, belongs to *Vascoceras nigeriense* Woods, 1911. The lectotype is a smooth end member of the species, as are the individuals referred by Meister (1989) to *Paravascoceras nigeriense*? (Woods) and *Vascoceras ellipticum* Barber.

Smooth examples of *Pseudovascoceras nigeriense* have in the past been compared with *Vascoceras gamai* (Barber 1957: 15; Hancock & Kennedy 1981: 357). Their similarity concerns only the outer whorls, however, and is homeomorphic in nature. Ornamented examples of *P. nigeriense* share similarities with various genera. Meister (1989) referred forms in which the siphonal tubercles disappear early in ontogeny to *Paramammites,* which he regarded as a senior synonym of *Spathites (Jeanrogericeras)* Wiedmann, 1960 (type species *Ammonites reveliereanus* Courtiller, 1860). As mentioned above, this material cannot be referred to *Paramammites* or *Jeanrogericeras* as neither shows siphonal tubercles at any growth stage (see Choffat 1898: 64; Pervinquière 1907: 336; Wiedmann 1960: 741; Renz 1982: 84; Berthou *et al.* 1985: 62) and resemblances are superficial only. Some of the present specimens have the appearance of giant *Protacanthoceras proteus* (compare Fig. 23 and Wright & Kennedy 1980: fig. 5). Others with dense, multiple ventral ribbing resemble *Kamerunoceras* Reyment, 1954*b* (type species *Acanthoceras eschii* Solger, 1904) or *Euomphaloceras* Spath, 1923 (type species *Ammonites euomphalus* Sharpe, 1855), though they lack the typically euomphaloceratine constrictions upon their early whorls. In its style of ribbing and the generally coarse nature of the tuberculation, the present material most closely resembles *Cunningtoniceras* Collignon, 1937 (type species *Ammonites cunningtoni* Sharpe, 1855). This is mainly a Middle Cenomanian genus (see, for example, Kennedy 1971, Zaborski 1985, Kennedy & Cobban 1990*a*) but it ranges into the Upper Cenomanian (Wright & Kennedy 1987, Cobban *et al.* 1989, Kennedy & Cobban 1990*b*). *Pseudovascoceras* may be a descendant of *Cunningtoniceras*. Introduction into north-eastern Nigeria produced peramorphic individuals losing their ornament early in ontogeny and coming to resemble *Vascoceras*. Interestingly there is a morphological overlap between *P. nigeriense* and *Nigericeras ogojaense* Reyment (1955: 62, pl. 13, fig. 6; pl. 14, fig. 3; text-fig. 28); the two are probably conspecific. The latter comes from the southern, oceanward, end of the Benue Trough where smooth individuals are unknown; the holotype (C.47401) and newly collected material (C.93578-61) all show prominent ornament.

Reyment (1979, 1988) has remarked upon the extraordinary polymorphism that may be displayed by vascoceratid species. He believed that in the changeable environment of the Cenomanian-Turonian intracontinental sea in west and Saharan Africa selection would have favoured forms with genetic or phenotypic flexibility. Such taxa would have been capable of responding to environmental fluctuations, each morphotype being best suited to a particular kind of environment. Meister *et al.* (1992) took up this issue in respect of the Niger ammonites. They noted that particular stratigraphical horizons there commonly yield monospecific faunas or assemblages dominated by one species. They speculated that taxa able to occupy niches in the exacting environments prevailing during the Late Cenomanian and Early Turonian faced virtually no competition, the result being a high degree of polymorphism. In unit O at Ashaka a number of ammonite taxa co-exist, largely as a result of introduction of species during a marine flooding episode. While there is some overlap, however, each of the four main taxa described here, *Paravascoceras cauvini*, *Vascoceras bullatum*, *V. globosum costatum* and *Pseudovascoceras nigeriense*, occupies a particular part of the morphological spectrum (Fig. 12). Variation in gross shell proportions to the extent of that suggested by Meister *et al.* (1992) for *P. cauvini* in Niger is not seen in these taxa. On the other hand, within *P. nigeriense* there seems to have been virtually no selection pressure favouring any particular strength of ornamentation. In this respect the polymorphic potential of the species was capable of wide expression. Much the same can be said of *Fikaites varicostatus* Zaborski, the other strongly ornamented form found in some numbers in unit O at Ashaka. This species shows a significant variation in the strength of its ribbing and tuberculation (see Zaborski 1993).

Family **VASCOCERATIDAE** Douvillé, 1912
Subfamily **VASCOCERATINAE** Douvillé, 1912
Genus ***VASCOCERAS*** Choffat, 1898

(= *Discovascoceras* Collignon, 1957; *Greenhornoceras* Cobban & Scott, 1972; *Provascoceras* Cooper, 1979)

TYPE SPECIES. *Vascoceras gamai* Choffat, 1898; by the subsequent designation of Roman, 1938.

REMARKS. Choffat (1898: 51–53) had a broad concept of *Vascoceras* as encompassing forms basically united by the possession of a simple suture pattern. Some of these original members are now referred to *Spathites* Kummel & Decker, 1954. The type species, *V. gamai*, was regarded as part of a group characterized by a wide umbilicus and the possession of a single (umbilical) row of tubercles. Recent discussions of *Vascoceras* have been given by Wright & Kennedy (1981) and Berthou *et al.* (1985). It is commonly suggested that *Paravascoceras*, *Pachyvascoceras*, *Paracanthoceras*, *Broggiiceras*, *Discovascoceras*, *Provascoceras* and, sometimes, *Greenhornoceras* should be regarded as strict synonyms of *Vascoceras* without even subgeneric distinction (see Berthou *et al.* 1985, Kennedy, Wright & Hancock 1987, Luger & Gröschke 1989, Kennedy, Cobban, Hancock & Hook 1989, Cobban *et al.* 1989).

The oldest known species included in *Vascoceras* is the micromorph *Ammonites diartianus* d'Orbigny, the type material of which was redescribed by Kennedy & Juignet (1977). Further examples were subsequently described by Wright & Kennedy (1981: 86, pl. 17, fig. 1; text-figs 29A–F), Förster *et al.* (1983: 133, pl. 3, figs 1–5) and Cobban *et al.* (1989: 47, figs 48, 88TT-AA). *V. diartianum* occurs most frequently in the Geslinianum Zone or equivalents but Kennedy *et al.* (1989: 80) reported examples in New Mexico from equivalents of the underlying Guerangeri Zone. Kennedy & Wright (1985) and Wright & Kennedy (1987) drew attention to the morphological similarity between *V. diartianum* and *Protacanthoceras* of the *P. proteus* Wright & Kennedy group (see Wright & Kennedy 1980: 95, figs 49–51, 57–58; 1987: 216, pl. 55, figs 4, 9, 17, 18, 21–23; text-figs 82B, 83G, M, 84P). They believed the former to have been derived from the latter. Accordingly, *V. diartianum* would constitute the root stock of *Vascoceras* and the above-mentioned suggested synonyms.

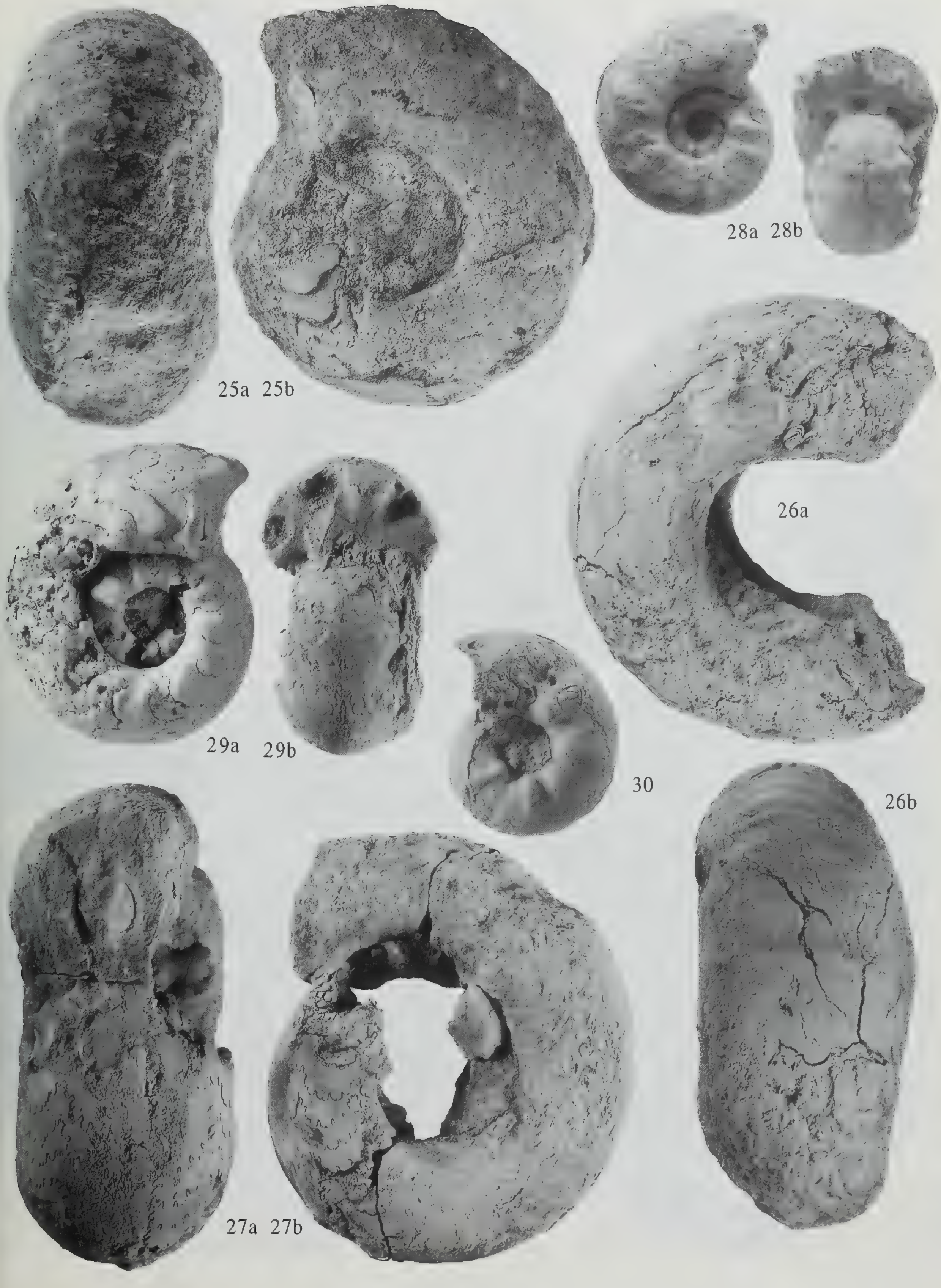
Cooper (1979) was reluctant to admit the Late Cenomanian age of *Vascoceras* and pointed to a number of differences between *Ammonites diartianus* and *V. gamai*, the most significant of which regarded their ornamentation. He proposed the genus *Provascoceras* for *A. diartianus* but regarded the species as ancestral to both *Vascoceras* and *Paravascoceras*. *A. diartianus* is clearly transitional between Acanthoceratinae and Vascoceratidae, retaining the bifid first lateral saddle of the former. Its ornament consists of rounded to twisted to distinctly bullate umbilical tubercles which may envelop practically the whole of the flanks and fine bundled ribbing extending across the venter. Relatively little is known of the inner whorls of topotype material of *V. gamai*. Choffat (1898: pl. 7, figs 3, 4; pl. 8, fig. 4; pl. 10, fig. 2) figured a number of juveniles which show approximately 8 umbilical bullae and 20 coarse, regularly developed major and minor ribs which cross the venter (see also Berthou *et al.* 1985: 67). The umbilical tubercles may be persistent but the ornament generally disappears on the later whorls. A similar juvenile ornament has been described in material referred to *V. gamai* from Egypt (Luger & Gröschke 1989: 378, pl. 40, figs 5, 7) and *V.* cf. *gamai* from New Mexico (Cobban *et al.* 1989: 45, figs 87W-AA, EE-RR). There are, however, other juveniles from Portugal with rather different ornamentation. *V. silvanense* Choffat (1898: 57, pl. 8, fig. 5; pl. 21, fig. 9) shows massive umbilical bullae but no definite ribbing. Berthou *et al.* (1985: 68) regarded *V. silvanense* as a *nomen dubium* and almost certainly the inner whorls of one or another of the Portugese species of *Vascoceras*. Another individual (Berthou *et al.* 1985: 68, pl. 3, figs 4, 8, 9) displays about 10 umbilical bullae intermediate in strength between those found in *V. gamai* and *V. silvanense* and about twice as many low ventral ribs mostly arising in pairs from these bullae. Berthou *et al.* (1985: 68) compared this specimen with *V. adonense* Choffat which they regarded as a synonym of *V. gamai*. Its ornament is reminiscent of that in *Ammonites diartianus*. Numerous juvenile whorls of *V. woodsi* are available from north-eastern Nigeria (see below). They show a considerable variation in ornament. Although no comparable variation series is available for the Portugese *Vascoceras*, it is possible that certain *V. gamai* could show an early ornament approaching that in *Ammonites diartianus*. Despite its transitional nature, *A. diartianus* is here regarded as belonging in *Vascoceras* and *Provascoceras* is therefore a synonym.

Discovascoceras Collignon (type species *Vascoceras (Discovascoceras) tesselitense* Collignon 1957: 125, pl. 1, figs 1a, b; by original designation) was originally proposed by Collignon (1957: 123) as a subgenus of *Vascoceras* but was later raised to the status of a separate genus following an amended diagnosis (Collignon 1965: 179). Its essential characters were given as its triangular whorls, presence of three carinae on the middle whorls, variation in spacing and degree of indentation of the sutures, depth of the umbilicus, egression of the adult whorl and tendency for apertural constriction. Berthou *et al.* (1985: 75) regarded the holotype of *D. tesselitense* as an indeterminate *Vascoceras*, the species as invalid and *Discovascoceras* Collignon, 1957 as a synonym of *Vascoceras*. In view of its ventral carinae they compared the material later described as *D. tesselitense* by Collignon (1965: 181, pl. G, figs 1a, b) with *Pseudotissotia* Peron (see also Hirano 1983: 69–70). They proposed that Collignon's second account be taken as the first valid one of *Pseudotissotia*? *tesselitense*. Collignon's (1965) material, however, shows similarities with Nigerian forms intermediate between *Vascoceras globosum costatum* and *Thomasites* which are described below. Here both the Collignon 1957 and 1965 descriptions are regarded as dealing with *Vascoceras* but the 1965 material could alternatively be assigned to *Thomasites*.

Greenhornoceras Cobban & Scott (type species *Vascoceras (Greenhornoceras) birchbyi* Cobban & Scott 1972: 85, pl. 22; pl. 23, figs 1–13; pl. 24, figs 1–12; pl. 25; pl. 26, figs 5–8, 11, 12; pl. 27, figs 1–6; text-figs 43–47; by original designation) is amongst the stratigraphically youngest examples of *Vascoceras*. Cobban & Scott (1972: 84–85) distinguished the subgenus *Greenhornoceras* only on the basis of being more involute than *V. (Vascoceras)* and in maintaining a square to rectangular whorl section. Its juvenile ornament of strong, regularly developed long and short ribs gives way to smooth later whorls. There is no compelling reason to regard *Greenhornoceras* as anything other than a strict synonym of *Vascoceras*.

As mentioned above, *Paravascoceras* (= *Paracanthoceras*, *Pachyvascoceras*, *Broggiiceras*) is here regarded as a distinct genus with an origin separate from that of *Vascoceras* and is most properly included in the Acanthoceratinae.

Figs 25–30 *Vascoceras woodsi* sp. nov. Figs 25–27, Pindiga Formation, unit M, Ashaka. Fig. 25a, b, paratype, C.93341, ×1. Fig. 26a, b, paratype, C.93339, ×1. Fig. 27a, b, holotype, C.93342, ×1. Fig. 28a, b, Pindiga Formation, unit M, Pindiga. Paratype, C.91263, ×1. Fig. 29a, b, Pindiga Formation, unit N, Pindiga. Paratype, C.93351, ×1. Fig. 30, Pindiga Formation, Deba Habe. Paratype, C.91257, ×1.


25a 25b
28a 28b
26a
29a 29b
30
26b
27a 27b

Vascoceras woodsi sp. nov. Figs 9–11, 25–32

1957	*Vascoceras* sp. juv. Barber: 27, pl. 6, figs 2, 4, 7; pl. 27, figs 10–15.
?1965	*Vascoceras gamai* Choffat; Collignon: 185, figs 5–7.
1989	*Plesiovascoceras* aff. gr. *thomi* (Reeside) ou sp. nov. Meister: 11, pl. 4, figs 2, 3, 5; text-fig. 8.
1989	*Paravascoceras* gr. *evolutum* Schneegans; Meister: 14 (*pars*), pl. 5, fig. 4 (only); text-fig. 10.
1990*a*	*Vascoceras* gr. *evolutum* (Schneegans); Zaborski: 7.
1990*a*	*Vascoceras* sp. Zaborski: figs 9, 10.
1990*a*	*Vascoceras* sp. juv. Zaborski: figs 16–18, 20, 21.
1992	*Vascoceras* gr. *thomi* (Reeside) ou *evolutum* (Schneegans); Courville: pl. 5, fig. 1.
1993	*Vascoceras* sp. nov. aff. *gamai* Choffat; Zaborski: 365.
1995	*Vascoceras* sp. nov. aff. *gamai* Choffat; Zaborski: 54, 55.

HOLOTYPE. C.93342 (Fig. 27), Pindiga Formation, unit M, Ashaka.

PARATYPES. Thirty-four specimens, C.93339, C.93341, C.93343-4, C.93543, Pindiga Formation, unit M, Ashaka; C.91262-70, Pindiga Formation, unit M, Pindiga; C.91224-5, C.91311, C.91313-4, C.93351, Pindiga Formation, unit N, Pindiga; C.91256-61, C.93355, C.93596a–f, C.93597, Pindiga Formation, Deba Habe.

DIMENSIONS.

	D	Wb	Wh	U
C.93597	94	–	31 (33)	39 (41.5)
C.93351	60	34 (57)	22 (37)	21 (35)
C.91264	53	32 (60)	20 (38)	18 (34)
C.93355	52	31 (60)	18 (35)	20 (38.5)
C.91256	50	29 (58)	20 (40)	17 (34)
C.91263	40	25 (62)	15 (37.5)	13 (32.5)
C.91257	39	24 (61.5)	16 (41)	11 (28)
C.91262	34	20 (59)	13 (38)	10 (29)

DERIVATION OF NAME. After the late H. Woods who first described ammonites from north-eastern Nigeria.

DIAGNOSIS. Evolute *Vascoceras* with whorls broader than high. Middle whorls with rounded or more normally highly bullate umbilical tubercles fusing with inner ventro-lateral bullae to cover the flanks. Adult body-chamber smooth or with umbilical tubercles and/or relatively weak ventral ribbing.

DESCRIPTION. The shell is evolute, the umbilicus widening during growth from about one-third to 40% or more of the overall diameter. The maximum diameter attained is about 120 mm, when the body-chamber makes up two-thirds of the final whorl. In all but the very earliest growth stages the whorls are distinctly broader than high.

Two nuclei are available. In C.93596f the whorls are initially smooth and tubular with a broadly rounded venter. At a diameter of 3 mm broad bullate swellings enveloping the inner half of the flanks appear and give rise to low ribs which cross the venter. The suture shows a direct transition from an entire to an evenly frilled E/L; this saddle is never bifid. In C.93596e about 10 umbilical bullae have developed by a diameter of 6 mm but the venter lacks ribbing.

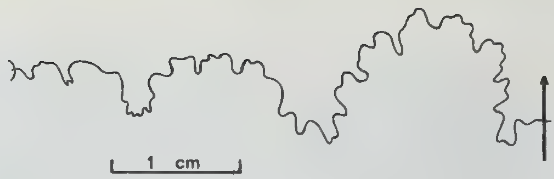


Fig. 31 Suture in *Vascoceras woodsi* sp. nov. Holotype, C.93342. Pindiga Formation, unit M, Ashaka.

In the succeeding growth stages (Figs 9, 10) the characteristic ornament consists of 8–10 lateral bullae in each whorl, upon which discrete umbilical and inner ventrolateral swellings can sometimes be made out. Most of the bullae give rise to a narrow rounded rib which crosses the venter and bears outer ventrolateral tubercles. No definite siphonal tubercles can be made out. There may be a single ventral rib bearing only outer ventrolateral tubercles alternating with each major rib. In other specimens no well-developed ribbing exists. In all cases sharply defined ribbing disappears at diameters of 10–15 mm though the lateral bullae persist. At these diameters the venter becomes flattened and the whorls increasingly depressed.

At diameters of 20–60 mm the main ornament consists of 6–8 umbilical tubercles in each whorl which are of variable shape and strength. They are commonly highly bullate but may be rounded, clavate or paired in nature. At first the more bullate types may partially fuse with bullate inner ventrolateral swellings but the latter features quickly fade during growth. Broad, vague fold-like ribs which cross the venter may issue from the umbilical tubercles or the venter may be smooth. Such ribs, however, rarely persist beyond diameters of 40 mm.

Umbilical tubercles may persist onto the adult body-chamber which is frequently compressed. Ventral ribbing may develop here taking the form of irregular closely-spaced plicae at one extreme and moderately strong fairly evenly-spaced ribs at the other.

The suture (Fig. 31) is of the typically simple type found in *Vascoceras*.

REMARKS. In a previous account (Zaborski 1990*a*: 5) doubt was expressed about whether a number of juvenile *Vascoceras* collected from Deba Habe and Pindiga were conspecific. *V. woodsi* has been found at these two localities and at Ashaka. At Pindiga adult specimens are not found, only the middle septate whorls being found in units L, M and N. At Ashaka the species is abundant in units K and, especially, M but the material consists almost entirely of poorly preserved adult body-chambers. At Deba Habe, however, specimens representing all growth stages occur in a 10 cm limestone less than 1 m below the level at which *Vascoceras globosum costatum* and *Pseudovascoceras nigeriense* appear. Occasional juveniles from Ashaka fit comfortably within the morphological range exhibited by the Pindiga and Deba Habe material. There is little doubt that all these specimens are conspecific.

Fig. 32 *Vascoceras woodsi* sp. nov. Pindiga Formation, Deba Habe. Paratype, C.93597, ×1.

Figs 33–35 *Vascoceras bullatum* Schneegans. Pindiga Formation, unit O, Ashaka. Fig. 33a, b, C.93512, ×1. Fig. 34a, b, C.93516a, ×1. Fig. 35a, b, C.93514, ×1.

Figs 36–37 *Pseudovascoceras nigeriense* (Woods). Pindiga Formation, unit O, Ashaka. Fig. 36a, b, C.93499, ×1. Fig. 37a, b, C.93494d, ×1.


32
36a
33a
36b
34a
34b
33b
37a
37b
35a
35b

Adult *V. woodsi* are closely similar to *V. gamai* Choffat (1898: 54, pl. 7, figs 1–4; pl. 8, fig. 1; pl. 10, fig. 2; pl. 21, figs 1–4; see also Berthou *et al.* 1985 for a revision of the species). The strong regular ribbing of the early whorls in *V. gamai* figured by Choffat (1898: pl. 7, figs 3, 4; pl. 8, fig. 4; pl. 10, fig. 2), however, differs from the ornament at the same stages in *V. woodsi*. It should be noted that certain juvenile specimens from Portugal show similarities with some Nigerian individuals: compare C.91264 (Fig. 11) with *V. silvanense* Choffat (1898: pl. 8, fig. 5), and C.93351 (Fig. 29) with Berthou *et al.* (1985: pl. 3, figs 4, 8, 9). A more complete knowledge of the early whorls in *V. gamai* is necessary for full comparison with *V. woodsi*.

Closer to the Nigerian juveniles is *V. diartianum*, particularly material from Germany which reaches diameters of over 30 mm (see Förster *et al.* 1983). This collection includes individuals with rather rounded umbilical tubercles (Förster *et al.* 1983: pl. 3, fig. 1; compare with Zaborski 1990*a*: fig. 20) and others with highly bullate umbilical tubercles similar to those common in *V. woodsi* (compare Förster *et al.* 1983: pl. 3, figs 2–5 and C.91263, C.91257, Figs 28, 30 herein). *V. woodsi* is a little younger than *V. diartianum* and derivation from the latter can easily be imagined by peramorphosis and further simplification of suture pattern.

The material from Ashaka described by Meister (1989: 11, pl. 4, figs 2, 3, 5; text-fig. 8) as *Plesiovascoceras* aff. gr. *thomi* (Reeside) belong in *V. woodsi*; *Vascoceras thomi* Reeside (1923) is a synonym of *Fagesia catinus* (Mantell) (see also Wright & Kennedy 1981: 88, 97). Those he referred to *Paravascoceras* gr. *evolutum* Scheegans are partly *V. woodsi* (Meister 1989: pl. 5, fig. 4) and probably partly *Pseudaspidoceras pseudonodosoides* (Choffat) (Meister 1989: pl. 5, fig. 2). *Paravascoceras cauvini* var. *evoluta* Schneegans (1943: 130, pl. 8, fig. 2) is here considered to be a strict synonym of *Paravascoceras cauvini*.

Specimens of *Vascoceras* described by Zaborski (1990*a*: 5, figs 9, 10) are further examples of *V. woodsi*. They were incorrectly reported as having come from the Gadeni Zone at Pindiga but are from large exotic blocks derived from unit N upstream and not from the immediately adjacent unit A.

Specimens from the Algerian Sahara referred to *V. gamai* by Collignon (1965: 185, figs 5–7) are a very close match for adult *V. woodsi* and may be conspecific. Unfortunately their inner whorls are completely unknown.

Vascoceras bullatum Schneegans, 1943

Figs 13, 33–35

1943 *Paravascoceras crassus* (Furon) var. *bullata* Schneegans: 131, pl. 8, figs 3, 4.
1989 *Paravascoceras crassum* (Furon); Meister: 18, pl. 6, figs 2, 3; text-fig. 12.
1989 *Paravascoceras carteri* (Barber); Meister: 21 (*pars*), pl. 9, fig. 1 (only).
1992 *Vascoceras* gr. *crassum* (Furon) ou *costellatum* Collignon; Courville: pl. 5, fig. 2; pl. 6, fig. 1.

MATERIAL AND OCCURRENCE. Eleven specimens, C.93508-15, C.93516a–c, Pindiga Formation, unit O, Ashaka.

DIMENSIONS. See Fig. 12.

REMARKS. Members of this species are relatively evolute and generally show markedly depressed whorls with a rounded to subtriangular outline. Umbilical bullae may or may not be present. The evenly frilled sutures are characterized by a broad low E/L and a narrow L.

Most individuals are readily recognizable due to the development of regular ribbing on the flanks and venter during their middle ontogenetic stages. The ribs may be coarse and rounded but vary to finer, denser structures in other individuals. Although this ribbing may be developed at diameters of less than 20 mm, some specimens remain smooth throughout ontogeny (see Fig. 13; Meister 1989: pl. 9, fig. 1). Regularly developed ribbing may be a transient feature which disappears or weakens greatly on the later septate whorls. The more involute members of the species overlap in shell proportions with certain *Vascoceras globosum costatum* and *Pseudovascoceras nigeriense* (see Fig. 12) and such individuals may be difficult to differentiate if they lack ribbing.

The juvenile whorls are not distinctive. They are often only moderately depressed and are smooth or ornamented with umbilical bullae alone (Fig. 34).

The adult body-chamber makes up between two-thirds and three-quarters of the final whorl. It may be smooth but generally shows an irregularly developed ornament of coarse, rounded fold-like to denser, sharper, narrow crease-like ribbing on the venter and outer flanks. Meister (1989: 18) pointed out that the body-chamber becomes constricted but the adult aperture itself is flared (Fig. 35). This modification occurs at diameters between 73 mm and 110 mm. There is no clear evidence of size dimorphism, however; other individuals showing a flared aperture do so at diameters of 80, 82, 82, 85, 85, 85, 86, 88, 95, 97, 98, 100 and 104 mm. Cobban & Hook (1983) described a large population sample of *Neoptychites cephalotus* (Courtiller) from New Mexico which shows similar adult body-chamber modifications. They too found that adult sizes were highly variable with no discernible bimodal pattern.

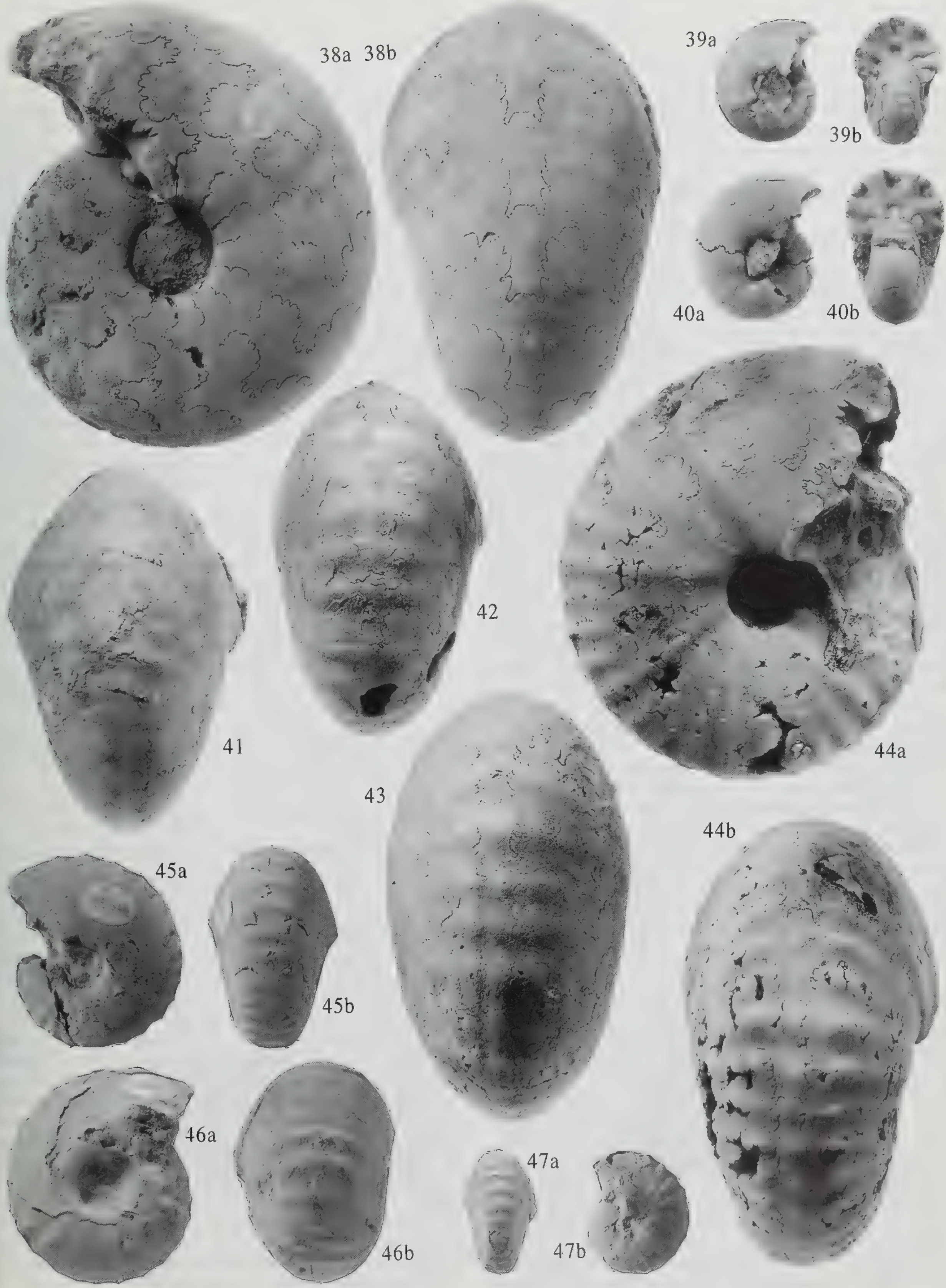
Paravascoceras crassus var. *bullata* Schneegans (1943: 131, pl. 8, figs 3, 4) has depressed whorls and ribbing of a closely similar style to that in the present material. Its umbilicus, representing about 25% of the overall diameter, is narrower than the average in the Nigerian forms described here but in this respect there is an overlap with the more involute individuals (see Fig. 12). Schneegans (1943) regarded his material as a variety of *Vascoceras (Pachyvascoceras) crassus* Furon (1935: 58, pl. 3, figs 2a, b; text-fig. 17), a slightly less depressed and less evolute form. *V. (P.) crassum* shows only a very weak ornament of fine riblets though its suture pattern is close to that in the present material. As mentioned above, *V. (P.) crassum* may be most properly referred to *Paravascoceras*. In view of the clear similarities between the present material and *Pachyvascoceras crassum* var. *bullatum*, however, the name *Vascoceras bullatum* Schneegans is applied to it. The Nigerian material is distinct from coeval *Paravascoceras cauvini* and is therefore referred to *Vascoceras* rather than *Paravascoceras*, although with some uncertainty.

Paravascoceras costatum multicostatum Barber (1960: 60, pl. 13, fig. 3; pl. 14, figs 1, 2) combines the relatively open umbilicus

Figs 38–40 *Vascoceras globosum costatum* (Reyment). Pindiga Formation, unit O, Ashaka. Fig. 38a, b, C.93527, ×1. Fig. 39a, b, C.93536b, ×1. Fig. 40a, b, C.93536c, ×1.

Figs 41–44 *Thomasites gongilensis* (Woods). Pindiga Formation, unit O, Ashaka. Fig. 41, C.93582, ×1. Fig. 42, C.93579, ×1. Fig. 43, C.93580, ×1. Fig. 44a, b, C.93583, ×1.

Figs 45–47 *Vascoceras globosum proprium* (Reyment). Pindiga Formation, unit T2, Ashaka. Fig. 45a, b, C.93548, ×1. Fig. 46a, b, C.93551, ×1. Fig. 47a, b, C.93547, ×1.


38a 38b
39a
39b
40a
40b
41
42
43
44a
44b
45a
45b
46a
46b
47a
47b

and dense ribbing style of *V. bullatum* with the whorl proportions and suture pattern of *V. globosum costatum*. Material of this kind has not been found in the present study and its precise affinities are uncertain.

Vascoceras rumeaui Collignon (1957) has an ornament of strong ribs similar to that in *V. bullatum* but is less depressed. As discussed above, it may be more closely related to *Paravascoceras cauvini*. *V. durandi* Choffat and the doubtfully distinct *V. kossmati* Choffat (see Berthou *et al.* 1985 for a review) are both depressed, relatively evolute species but lack the marked ribbing and adult apertural modifications seen in *V. bullatum*.

Vascoceras globosum (Reyment, 1954*b*)

REMARKS. This species was discussed by Kennedy *et al.* (1987: 46). They brought into synonymy a large amount of material described from Nigeria and elsewhere including *Pachyvascoceras globosum* Reyment (1954*b*) and *Pachyvascoceras proprium* Reyment (1954*b*) under the name *Vascoceras proprium* (Reyment, 1954*b*). Barber (1957: 21–27), however, had already treated the above two forms as conspecific and selected *Vascoceras globosum* (Reyment, 1954*b*) as the species name. *V. globosum* accordingly has priority over *V. proprium* and should replace it. Nigerian specimens assigned to the species are here referred to three subspecies as detailed below.

The *V. globosum* group shows a wide morphological variation and complex phylogenetic relationships. Early members of the group seem to include the ancestors of *Thomasites gongilensis* (Woods). Later members are characterized by rather complex sutures; *V. obscurum* and probably also *Neoptychites* Kossmat were derivatives.

The precise origin of *V. globosum* is obscure. There are no obvious ancestors within the north-eastern Nigerian sections. *V. woodsi* is a possibility but is more evolute and has a stronger, more persistent juvenile ornamentation. *Paravascoceras cauvini* is markedly more compressed while the inner whorls of its later members are entirely smooth, unlike those in *V. globosum costatum*.

Berthou *et al.* (1985: 72) suggested that *Vascoceras (Pachyvascoceras) crassus* Furon, 1935 was a senior synonym of *Pachyvascoceras costatum* Reyment, 1954*b* (= *V. globosum costatum*). Meister *et al.* (1992: 72, pl. 7, figs 1, 2, 4, 5) described formes from sections at Tanout Aviation and Birgimari in Niger as *Paravascoceras cauvini* of *V. crassum* type and others transitional from *V. crassum* to *V. proprium* type. The latter group could probably include their *V.* gr. *ellipticum* Barber (Meister *et al.* 1992: 76, pl. 7, fig. 3; pl. 8, figs 1, 2) from the same sections. These formes are associated with *Paravascoceras cauvini* of typical aspect. Schneegans (1943) also reported passage forms from *P. cauvini* to *V. crassum* in Niger. Meister *et al.* (1992: 74) discussed the possible relationships within the Niger faunas. They remarked that undoubted *V. proprium* (= *V. globosum*) had not been found in Niger, and speculated that the horizons with *P. cauvini* contained essentially monospecific ammonite faunas; this species produced a wide range of morphotypes with variable degrees of whorl compression and ornamental strength. According to this interpretation *V. crassum* is a homeomorph of *V. globosum costatum*, the first a member of the *P. cauvini* group, the latter having a separate origin. In support it may be noted that unit O at Ashaka, in which *V. globosum* appears, also contains the abrupt first occurrences of *V. bullatum* and *Pseudovascoceras nigeriense*. The base of unit O is a marine flooding surface suggesting that its fauna is largely an introduced one, the ancestors of which lie outside north-eastern Nigeria. *Vascoceras (Pachyvascoceras) crassum* and *V. globosum* are here regarded as distinct from one another; the former, as stated above, is probably best referred to *Paravascoceras*.

Vascoceras globosum costatum (Reyment, 1954b)

Figs 38–40, 50

1954*b* *Pachyvascoceras costatum* Reyment: 257, pl. 3, fig. 6; pl. 4, fig. 3; pl. 5, fig. 2; text-figs 3a, b, 5.
1955 *Pachyvascoceras costatum* Reyment; Reyment: 65, pl. 14, figs 2, 4.
?1957 *Vascoceras robustum* Barber: 15, pl. 5, fig. 1; pl. 26, figs 5, 6.
?1957 *Vascoceras polygonum* Barber: 17, pl. 5, fig. 2; pl. 29, figs 1–3.
1957 *Paravascoceras costatum costatum* (Reyment) Barber: 35, pl. 14, fig. 1; pl. 32, figs 1–3.
1957 *Paravascoceras costatum quadratum* Barber: 35, pl. 16, fig. 2; pl. 32, figs 10, 11.
1957 *Paravascoceras costatum tectiforme* Barber: 37, pl. 14, fig. 4; pl. 15, figs 1, 3; pl. 16, fig. 2; pl. 32, figs 4–7.
1965 *Pachyvascoceras costatum* Reyment; Reyment: pl. 3, fig. 17.
1976 *Vascoceras robustum* Barber; Offodile & Reyment: 54, figs 23a, b.
1976 *Vascoceras ellipticum* Barber; Offodile & Reyment: 55, figs 25a, b.
1976 *Paravascoceras costatum* (Reyment); Offodile & Reyment: 55, figs 26a, b.
1976 *Paravascoceras tectiforme* Barber; Offodile & Reyment: 55, figs 29a, b.
1989 *Paravascoceras tectiforme* Barber; Meister: 21, pl. 7, figs 1, 2; pl. 8, figs 1–5; text-fig. 13.
1992 *Vascoceras tectiforme* (Barber) *sensu* Meister; Courville: pl. 7, figs 1, 2.

MATERIAL AND OCCURRENCE. Twenty-six specimens, C.93310, C.93519-34, C.93535a–d, C.93536a–e, Pindiga Formation, unit O, Ashaka.

DIMENSIONS. See Figs 12, 48.

REMARKS. The phragmocone in *V. globosum costatum* reaches a diameter in excess of 130 mm, making it the largest member of the genus known in north-eastern Nigeria. Whorl breadth is slightly to distinctly greater than whorl height while the umbilicus represents 15–28% of the total diameter. In overall shell proportions *V. globosum costatum* overlaps with *V. bullatum* and *Pseudovascoceras nigeriense* and smoother individuals of these two species may be difficult to distinguish from it, especially in their middle growth stages.

At diameters of less than 30 mm (Figs 39, 40) the whorls in *V. globosum costatum* are weakly ornamented. Some forms are virtually smooth, others display umbilical tubercles but most commonly there are weak, broadly rounded ribs, most pronounced ventrally and sometimes with traces of bullate ventrolateral tubercles. The whorls tend to be more compressed in the early than in the later growth stages.

In the middle whorls ornament may be lacking or there may be broad, low ventral ribs. Umbilical tubercles persist in some individuals. In the adult stages irregular fold-like ribs may appear, especially upon the venter. The range of shell shapes and ornamentation is well displayed by the abundant previously described material (see synonymy list).

Suture patterns are of the typically simple type characteristic of *Vascoceras*.

Barber (1957), Meister (1989) and Courville (1992) separated forms of *V. globosum costatum* with subtriangular to triangular whorl sections as *Paravascoceras costatum tectiforme* Barber, *P. tectiforme* Barber and *Vascoceras tectiforme* (Barber). In unit O at Ashaka there is a complete intergradation of forms with rounded and triangular whorl sections. The latter themselves show rounded venters in their early growth stages. This shape variation is attributed no taxonomic significance here.

Of greater interest is the fact that *V. globosum costatum* shows a gradation into *Thomasites* at the same stratigraphical level at Ashaka. A variation series is shown in Figs 41–44, 50. This encompasses more or less smooth forms with ovoid to subtriangular whorls (Figs 41, 50) through forms with weak but definite ventral tubercles and incipient carinae (Figs 42, 43), into strongly ornamented individuals (Fig. 44) occurring in the upper part of the unit and well within the morphological range of *Thomasites gongilensis* (Woods) (see faunas described by Barber 1957, Meister 1989). The *Neoptychites cephalotus* (Courtiller) of Meister (1989: 12, pl. 4, fig. 4) and *Thomasites* sp. nov.? of Courville (1992: 420, pl. 10, fig. 4; pl. 12, fig. 1) are further examples of early *Thomasites*. *V. globosum costatum* seems to contain the ancestors of *T. gongilensis*, a species which reaches its acme in unit R at Ashaka where it forms the bulk of the ammonite fauna.

The *Paravascoceras* aff. *chevalieri* (Furon) of Reyment (1955: 53, pl. 14, figs 1a, b) from southern Nigeria also shows three rows of ventral tubercles and resembles the early *Thomasites* from Ashaka. The same can be said of the material of *Discovascoceras tesselitense* described by Collignon (1965: 181, pl. G, figs 1a, b) which shows three ventral carinae, subtriangular whorls and a deep, fairly narrow umbilicus. Hirano (1983) and Berthou *et al.* (1985) compared this material with *Pseudotissotia*, but it appears closer to the Nigerian forms transitional from *Vascoceras to Thomasites* described here.

Vascoceras globosum globosum (Reyment, 1954b)

Figs 51, 52

1954*b* *Pachyvascoceras globosum* Reyment: 259, pl. 3, fig. 3; pl. 4, fig. 4; text-figs 3e, 7.
1957 *Vascoceras globosum globosum* (Reyment) Barber: 21 (*pars*).
1957 *Vascoceras globosum carteri* Barber: 25, pl. 8, fig. 2; pl. 28, figs 8, 9.
1965 *Vascoceras carteri* Barber; Reyment: pl. 3, fig. 12.
1976 *Paravascoceras carteri* (Barber) Offodile & Reyment: 55, figs 27, 28.
1989 *Paravascoceras carteri* (Barber); Meister: 21 (*pars*), pl. 9, fig. 3 (only); pl. 10, figs 1, 2; text-fig. 14.
1992 *Vascoceras tectiforme* (Barber) *sensu* Meister; Courville: pl. 7, fig. 3 (only).
1992 *Vascoceras* gr. *globosum* (Reyment) ou *Fagesia* sp. Courville: pl. 8, figs 1, 2.
?1992 *Vascoceras* sp. aff. *obscurum* Barber; Courville: pl. 10, fig. 3 (only).

MATERIAL AND OCCURRENCE. Three specimens, C.93544-6, Pindiga Formation, unit R, Ashaka. The form also occurs in unit O at Ashaka and unit O at Pindiga.

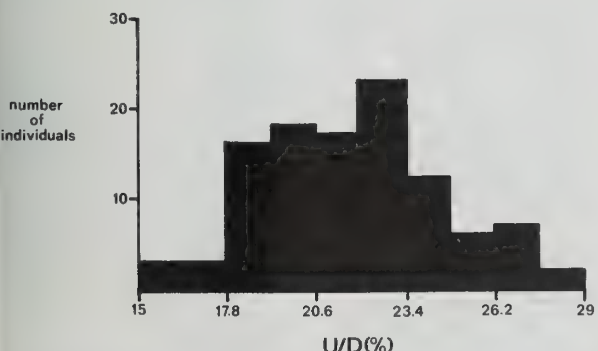
DIMENSIONS. See Figs 12, 48.

REMARKS. *V. globosum globosum* is characterized by its highly depressed whorls which are at least twice as broad as high. Although such forms occur throughout the range of *V. globosum* in north-eastern Nigeria there are morphological and stratigraphical reasons for considering the earlier individuals as a separate subspecies. In unit O at Ashaka highly depressed examples of *V. globosum* are rare but those that occur fall well outside the morphological range of *V. globosum costatum* (see Figs 12, 48). In both unit R at Ashaka and unit O at Pindiga *V. globosum globosum* is the only member of the species that has been found. It is fairly frequent at these levels where the more compressed part of the morphological spectrum is occupied by large numbers of *Thomasites gongilensis*.

The juvenile whorls in *V. globosum globosum* show sharper ribbing than in *V. globosum costatum*. The ribs cross the flank, unlike in *V. globosum proprium* in which they are largely confined to the venter and outer flanks. Specimen C.93544 (Fig. 51) is a very close match for the holotype of *Pachyvascoceras globosum* (C.47408, see Reyment 1954*b*: pl. 3, fig. 3; pl. 5, fig. 4) which is also a juvenile.

Since details of the inner whorls are useful in identification it is difficult to determine which of the specimens described by Barber (1957: 21) as *V. globosum globosum* should be referred to that subspecies and which are depressed examples of *V. globosum proprium* (see below). His material appears to include both.

The sutures in *V. globosum globosum* are deeply incised; this appears to be a general feature of highly depressed *Vascoceras* which is shared with *V. harttii* (see below). Courville (1992: 421) drew attention to the suture pattern in *V. globosum globosum* and suggested that it may be better referred to *Fagesia* Pervinquière.



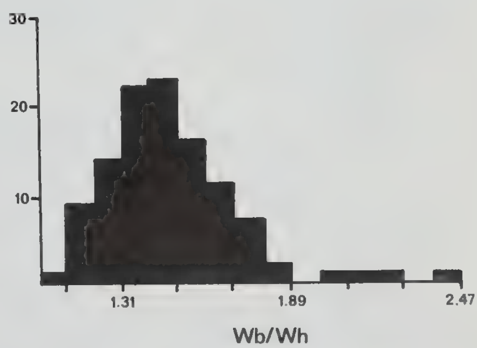


Fig. 48 Shell proportions in *Vascoceras globosum* (Reyment) occurring in unit O at Ashaka. Forms with a high Wb/Wh ratio are here assigned to *V. globosum globosum* (Reyment) (see also Fig. 12).

This genus, however, as well as being generally more evolute, shows a different ontogeny (see Zaborski 1987: 43 for a discussion). Its juvenile whorls characteristically show strong ribs arising in twos or threes from umbilical tubercles, elements of this ornament persisting to varying stages in later ontogeny. The present material shows an ontogenetic development typical of *Vascoceras* rather than *Fagesia*.

Barber (1957) proposed two species of *Fagesia* from north-eastern Nigeria but pointed out that they were both intermediate with *Vascoceras*. These forms are problematical, being based on a very few specimens of unknown stratigraphical provenance. *F. simplex* Barber (1957: 27, pl. 8, fig. 1; pl. 29, figs 4, 5) has a simple suture and is best regarded as an indeterminate *Vascoceras*. *F. involuta* Barber (1957: 27, pl. 9, fig. 3; pl. 29, figs 6, 7) has a complex suture, narrow umbilicus and highly depressed whorls; the early growth stages are unknown. It may be most closely related to *V. globosum globosum*.

Vascoceras globosum proprium (Reyment, 1954*b*)

Figs 45–47, 49, 55–57, 63, 64

1920 *Vascoceras angermanni* Böse: 217, pl. 16, figs 1, 3 (only); pl. 17, fig. 1.

1920 *Neoptychites* aff. *cephalotus* (Courtiller); Böse: 221, pl. 18, figs 3, 10, 13.

1931 *Thomasites* sp. Adkins: 56, pl. 2, figs 16, 17.

1954*b* *Pachyvascoceras proprium* Reyment: 258, pl. 5, figs 1a, b; text-fig. 3d.

1954*b* *Pachyvascoceras proprium plenum* Reyment: 258, pl. 5, fig. 5; text-figs 3c, 6.

1954*b* *Gombeoceras? bulbosum* Reyment: 263, pl. 4, figs 2a, b; text-figs 3g, 9.

?1957 *Vascoceras ellipticum* Barber: 17 (*pars*), pl. 6, figs 1a, b; pl. 26, fig. 11 (only).

1957 *Vascoceras globosum globosum* (Reyment) Barber: 21 (*pars*), pl. 7, fig. 1.

1957 *Vascoceras globosum plenum* (Reyment) Barber: 23, pl. 7, fig. 2; pl. 9, fig. 2; pl. 28, figs 3–5.

1957 *Vascoceras globosum proprium* (Reyment) Barber: 25, pl. 7, fig. 3; pl. 28, figs 6, 7.

1957 *Vascoceras globosum compressum* Barber: 25, pl. 7, fig. 4; pl. 9, fig. 1; pl. 28, figs 10, 11.

1963 *Pachyvascoceras compressum* (Barber) Powell: 321, pl. 32, figs 2–4, 7; pl. 34, figs 8, 10; text-figs 3b–d, f.

1963 *Pachyvascoceras globosum* Reyment; Powell: 321, pl. 34, figs 7, 11; text-fig. 3s.

1978 *Paravascoceras carteri* (Barber); Chancellor, Reyment & Tait: 92, figs 15–17.

1982 *Paravascoceras carteri* (Barber); Chancellor: 102, figs 35–37.

1982 *Paravascoceras compressum* (Powell not Barber) Chancellor: 106, figs 49, 50.

1987 *Vascoceras proprium* (Reyment); Kennedy, Wright & Hancock: 46, pl. 4, figs 1–15, 18, 19; pls 5, 6; text-figs 8A–C, 9.

1989 *Vascoceras (Vascoceras) proprium* (Reyment); Kennedy, Cobban, Hancock & Hook: 80, figs 20A, B.

1989 *Vascoceras* sp. juv. indet. Meister: pl. 11, fig. 3.

1992 *Vascoceras* sp. aff. *obscurum* Barber; Courville: pl. 10, fig. 2 (only).

MATERIAL AND OCCURRENCE. Eleven specimens, C.93365,

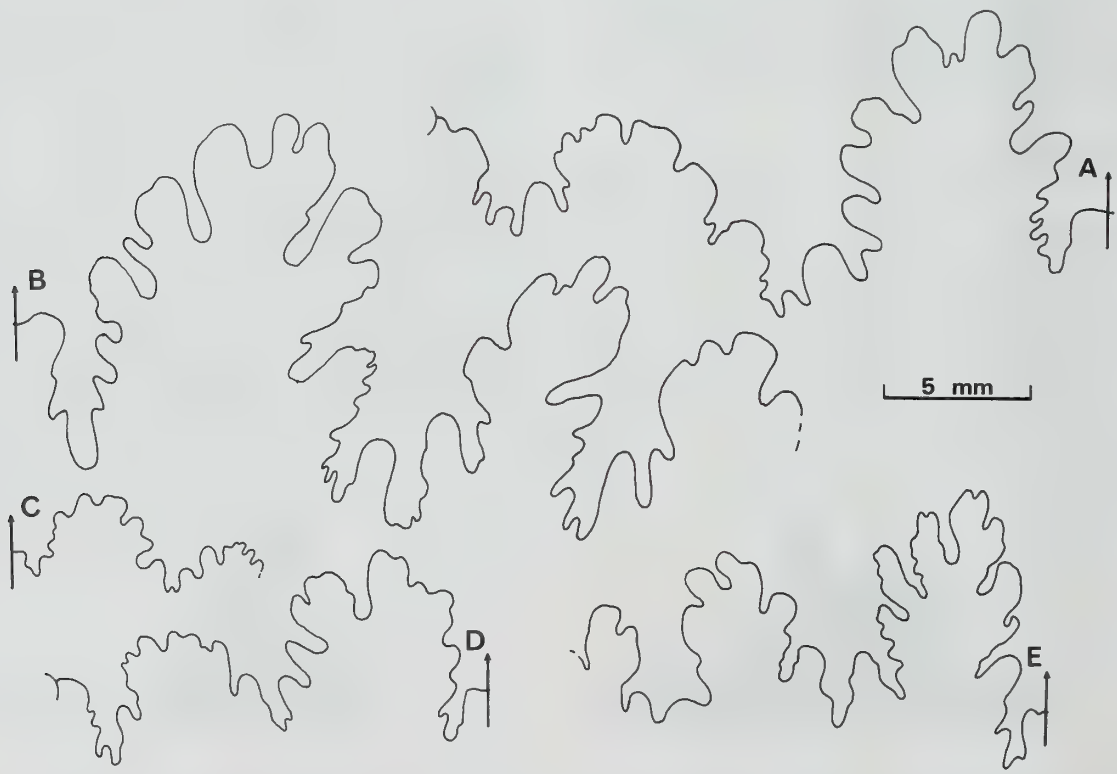


Fig. 49 Sutures in *Vascoceras globosum proprium* (Reyment). A, C.93550 at a diameter of 40 mm. B, C.93906 at a diameter of 54 mm. C, C.93905 at a diameter of 18 mm. D, C.93904 at a diameter of 30 mm. E, C.93549 at a diameter of 38 mm. All specimens from the Pindiga Formation, unit T2, Ashaka.

C.93547-51, C.93904-8, Pindiga Formation, unit T2, Ashaka. The subspecies also occurs in unit T1 at Ashaka.

DIMENSIONS.

	D	Wb	Wh	U
C.93365	64	48 (75)	32 (50)	13 (20)
C.93550	49	45 (92)	21 (43)	–
C.93549	46	30 (65)	21 (46)	–
C.93551	41	34 (83)	21 (51)	10.5 (26)
C.93548	37	23 (62)	17 (46)	6 (16)

REMARKS. *V. globosum proprium* is generally a distinctive form on account of its narrow umbilicus, representing 15–28% of the total diameter, its deeply incised sutures often showing elongate saddles (Fig. 49), and its juvenile ornament of sharp ribbing, almost always confined to the outer flanks and venter. Associated with the juvenile ribs there may be pronounced constrictions which persist until diameters of about 25 mm (Figs 53, 64). Umbilical bullae may or may not be present in the early growth stages. The material from unit T2 at Ashaka varies from moderately compressed (Fig. 45) to highly depressed forms (Fig. 57). The latter resemble the stratigraphically younger *V. globosum globosum*. Their juvenile ribbing style is closer to that in *V. globosum proprium*, however, and they are here treated as end members of that subspecies; similar variants occur in an assemblage of *V. globosum proprium* from Texas (Kennedy *et al.* 1987).

Some individuals have subdued ornamentation. The holotype of *Gombeoceras? bulbosum* Reyment (C.47295, Reyment 1954*b*: pl. 4, figs 2a, b) is a smooth *V. globosum proprium*.

The holotype of *Vascoceras ellipticum* Barber (C.47679, Barber 1957: pl. 6, figs 1a, b; pl. 26, fig. 11) is probably a further example of *V. globosum proprium*. Other individuals referred to *V. ellipticum* by Barber (C.47680-4) are of uncertain affinities. The example from Dukul (C.47633, Barber 1957: pl. 14, figs 1a, b; pl. 26, figs 3, 4) is an involute abraded specimen difficult to identify with certainty. After dissection many such forms found loose at Dukul prove to be *Thomasites gongilensis*.

Courville (1992: 424, pl. 10, fig. 2) reported a specimen of *V. globosum proprium* (his *V.* gr. *obscurum* Barber) from unit U (his Niveau 32) at Ashaka. The associated fauna described therein, however, is that typical of unit T2 (= upper part of his Niveau 30 at Ashaka. In the present work *V. globosum proprium* has been found only in unit T.

In its complex sutures and constricted inner whorls *V. globosum proprium* resembles *V. venezolanum* Renz (1982: 80, pl. 23, figs 5–11; pl. 24, figs 1–10; pl. 25, figs 1–8; text-fig. 61). The latter, highly variable species, however, generally shows denser, more persistent ribs which cross the flanks, although certain individuals may have subdued ribbing. *V. venezolanum* is known from southern Nigeria (Zaborski 1990*b*) but from beds containing *Mammites nodosoides* (Schlüter) which are younger than unit T at Ashaka.

Vascoceras obscurum Barber, 1957 — Figs 53, 54, 59, 61, 62

1957 *Vascoceras obscurum* Barber: 19, pl. 6, figs 3, 9; pl. 27, figs 16–18.
1989 *Vascoceras obscurum* Barber; Meister: 28, pl. 12, fig. 2; text-fig. 20.

MATERIAL AND OCCURRENCE. Five specimens, C.93552-3, C.93909-10, Pindiga Formation, unit T2, Ashaka; C.93326, Pindiga Formation, unit X, Ashaka.

DIMENSIONS.

	D	Wb	Wh	U
C.93909	64	29 (45)	31 (48)	6 (9)
C.93553	48	24 (50)	26 (54)	4 (8)
C.93326	44	21 (48)	24 (54.5)	4 (9)
C.93552	38	19 (50)	20 (53)	4 (10.5)

REMARKS. *V. obscurum* is a highly involute compressed species with a flattened to tabulate venter in its early stages which becomes rather more rounded during growth. The juvenile whorls bear strong regular ribs, some of which reach the umbilicus but which are mainly confined to the ventral region. The sutures are complex for the genus with fairly elongated highly frilled saddles (Fig. 59).

V. obscurum appears in unit T2 at Ashaka, occurring there alongside *V. globosum proprium*. A similar style of ribbing and complex suture pattern is present in these two forms. *V. obscurum* could be considered as an end member of *V. globosum proprium*. The consistently high degree of involution, the compressed whorls and the flattened venter, however, set *V. obscurum* apart while it has a different stratigraphical range than the latter form, being found in unit X at Ashaka. For these reasons *V. obscurum* is here treated as a discrete species, though it is clearly very closely related to *V. globosum proprium* from which it is probably derived.

The early whorls in *V. obscurum* resemble those in *V. pioti* (Peron & Fourtau) (see Freund & Raab 1969: 28, pl. 4, figs 1–9; text-figs 6d–g). The later growth stages, however, are unknown in the former, precluding comparison with the *Neoptychites*-like body-chamber in *V. pioti*.

In what is known of its morphology *V. obscurum* shows a close similarity to *Neoptychites*. Pronounced constrictions have not been seen in the available material but are found in the related *V. globosum proprium*. The *V. globosum proprium-V. obscurum* lineage may contain the root stock of *Neoptychites*.

Very similar to *V. obscurum* are the *Neoptychites* sp. juv. of Freund & Raab (1969: 47, pl. 8, figs 3–6) from Israel which occur well below the main stratigraphical range of the genus there.

Material from unit O at Ashaka referred to *Neoptychites* by Meister (1989: 12, pl. 14, text-fig. 4) is, as mentioned above, an early *Thomasites*. That described by Courville (1992: 421, pl. 12, fig. 2) from unit R as *Neoptychites* aff. *cephalotus* (Courtiller) is probably a member of the *V. globosum* group.

Vascoceras harttii (Hyatt, 1870) — Figs 58, 60

1870 *Ceratites harttii* Hyatt; 386.
1875 *Buchiceras hartti* (Hyatt) Hyatt: 370.
1887 *Ammonites (Buchiceras) harttii* (Hyatt); White: 226, pl. 19, figs 1, 2; pl. 20, fig. 3.
1903 *Vascoceras hartti* (Hyatt) Hyatt: 103, pl. 14, fig. 16.
1936 *Vascoceras hartti* (Hyatt); Maury: 247, pl. 22, figs 1, 2.
1978 *Paravascoceras hartti* (Hyatt) Chancellor, Reyment & Tait: 96, fig. 20.
1982 *Paravascoceras hartti* (Hyatt); Chancellor: 98, figs 28C, 29–33.
1985 *Vascoceras (Paravascoceras) harttii* (Hyatt); Howarth:


50a
51
52a
53a
53b
50b
52b
55a
54
55b
58a
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56b
57a
58b
57b

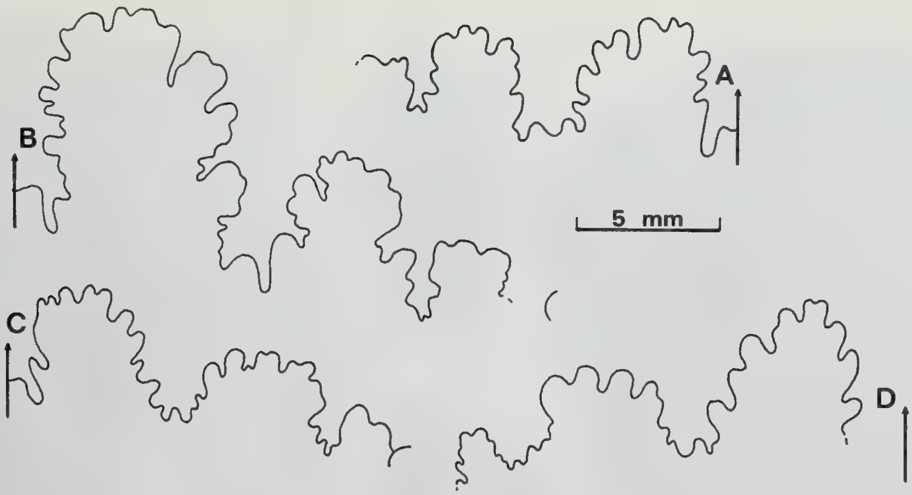

Fig. 59 Sutures in *Vascoceras obscurum* Barber. A, C.93910 at a diameter of 32 mm. B, C.93909 at a diameter of 45 mm. C, C.93552 at a diameter of 30 mm. D, C.93326 at a diameter of 34 mm. All specimens from the Pindiga Formation, unit T2, Ashaka except C.93326 which is from unit X at the same locality.

100, fig. 25 (with synonymy).
?1989 *Vascoceras hartti* (Hyatt); Cobban, Hook & Kennedy: 49, figs 49, 91A-D, G–K.
1989 *Fagesia superstes* var. *levis* Renz; Meister: 37, pl. 16, fig. 2; text-fig. 26.
1992 *Vascoceras* gr. *globosum* (Reyment) ou *Fagesia* sp.; Courville: pl. 9, fig. 1.

MATERIAL AND OCCURRENCE. Two specimens, C.93554-5, Pindiga Formation, unit X, Ashaka.

DIMENSIONS.

	D	Wb	Wh	U
C.93555	79	83 (105)	33 (42)	21 (26.5)
C.93554	49	50 (102)	21 (43)	12 (24.5)

REMARKS. These moderately evolute cadicones show sharp umbilical shoulders, which are undulating in C.93555, and steeply sloping umbilical walls. There are sharply rounded ventral ribs and occasional constrictions in C.93554 (Fig. 58) but they fade by a diameter of 40 mm leaving the internal mould smooth but for transverse growth striae. Neither specimen shows umbilical tubercles.

Kennedy *et al.* (1987: 51) pointed out the difficulty in distinguishing *V. hartti* from globose *V. globosum*. They regarded a more evolute coiling and a steeply sloping umbilical wall as most useful in identifying the former. In these respects the present material is more properly referred to *V. harttii* than the similar *V. globosum globosum*.

In the present work *V. harttii* has been found only in unit X at Ashaka. Meister (1989: 37–38) and Courville (1992: 424) also reported examples from unit U there which they referred to or compared with *Fagesia superstes* (Kossmat). As with *V. globosum globosum* (see above) these forms have an ontogenetic development characteristic of *Vascoceras* not *Fagesia*. The globose shape and complex suture pattern are not in themselves diagnostic of *Fagesia*.

STRATIGRAPHICAL AND PHYLOGENETIC DISCUSSION

The oldest ammonite-bearing beds in north-eastern Nigeria yield no vascoceratid taxa. They are characterized by *Nigericeras gadeni*, *Metengonoceras dumbli* (Cragin), *Placenticeras (Karamaites) cumminsi* Cragin and *Metoicoceras geslinianum* (d'Orbigny), the last species allowing correlation with the Geslinianum Zone in north-western Europe and the Gracile Zone of the western interior of the United States (see Kennedy 1984, Cobban 1984, Cobban *et al.* 1989). This '*Nigericeras* fauna' is widely recognizable in West and Saharan Africa (see Lefranc 1978, Meister *et al.* 1992).

Paravascoceras cauvini appears in unit E at Ashaka and becomes common in unit F there and in unit H at Pindiga. In the last two horizons it is associated with *Burroceras*? sp. (Zaborski 1995). Although not identifiable to species level this material may indicate correlation with the *Burroceras clydense* Zone of New Mexico. *P. cauvini* ranges through units K and M at Ashaka wherein *Vascoceras woodsi* occurs. These units also contain *Pseudaspidoceras pseudonodosoides*, on which basis they can be correlated with the Juddii Zone in the western interior. In south-western New Mexico a gap exists between the Juddii Zone and the basal Turonian Flexuosum Zone (Cobban *et al.* 1989). *Pseudaspidoceras flexuosum* Powell occurs in unit T2 at Ashaka. Units N to T1 at Ashaka belong to the Upper Cenomanian but

Fig. 50 *Vascoceras globosum costatum* (Reyment). Pindiga Formation, unit O, Ashaka. C.93523, ×1.
Figs 51, 52 *Vascoceras globosum globosum* (Reyment). Pindiga Formation, unit R, Ashaka. Fig. 51, C.93544, ×1. Fig. 52a, b, C.93545, ×1.
Figs 53, 54 *Vascoceras obscurum* Barber. Pindiga Formation, unit T2, Ashaka. Fig. 53a, b, C.93552, ×1. Fig. 54, C.93553, ×1.
Figs 55–57 *Vascoceras globosum proprium* (Reyment). Pindiga Formation, unit T2, Ashaka. Fig. 55a, b, C.93365, ×1. Fig. 56a, b, C.93549, ×1. Fig. 57a, b, C.93550, ×1.
Fig. 58 *Vascoceras harttii* (Hyatt). Pindiga Formation, unit X, Ashaka. C.93554, ×1.

Fig. 60 *Vascoceras harttii* (Hyatt). Pindiga Formation, unit X, Ashaka. C.93555, ×1.

Figs 61, 62 *Vascoceras obscurum* Barber. Fig. 61a, b, Pindiga Formation, unit X, Ashaka. C.93326, ×1. Fig. 62a, b, Pindiga Formation, unit T2, Ashaka. C.93909, ×1.

Figs 63, 64 *Vascoceras globosum proprium* (Reyment). Pindiga Formation, unit T2, Ashaka. Fig. 63a, b, C.93904, ×1. Fig. 64a–c, C.93905, ×1.

lack equivalents in south-western New Mexico. Unit O at Ashaka, which contains the youngest *Paravascoceras cauvini*, *Pseudovascoceras nigeriense*, *Vascoceras bullatum*, *V. globosum costatum* and *V. globosum globosum* is probably at least partially equivalent to beds with *Nigericeras scotti* in south-eastern Colorado.

Unit T2 at Ashaka contains an ammonite assemblage including *Pseudaspidoceras flexuosum* and *Vascoceras globosum proprium*. These forms occur together in the basal Turonian Flexuosum Zone in west Texas (Kennedy *et al.* 1987), *Thomasites* and *Wrightoceras munieri* (Pervinquière) also being associated in both places. *V. globosum proprium* is further recorded from New Mexico and Hancock (1991) suggested that it may serve as a better marker for the base of the Turonian than *Pseudaspidoceras flexuosum*. In the Ashaka section, however, it actually appears in unit T1 just below the first occurrence of *P. flexuosum*. A minor discontinuity representing a marine flooding surface separates units T1 and T2. The fauna of unit T2 seems to have in large part been introduced during this flooding event which may complicate the order of occurrence of these taxa at Ashaka.

Vascoceras obscurum ranges from the basal Turonian unit T2 into unit X at Ashaka. Units U to X at Ashaka, which also represent the known range of *V. harttii*, are of Early Turonian age. They cannot, however, be dated more precisely on the basis of their ammonite faunas which are almost entirely composed of *Pseudotissotia nigeriensis* (Woods) and *Eotissotia simplex* Barber. *V. harttii* has been assigned to the Lower Turonian in Angola (Howarth 1985), Brazil (Bengtson 1983) and Mexico (Chancellor 1982) but material from the Upper Cenomanian of New Mexico has also been referred to the species (Cobban *et al.* 1989: 49, figs 49, 91A–D, G–K).

With the exception of a few taxa 'vascoceratid' ammonites have not proved to be of great value in detailed correlation,

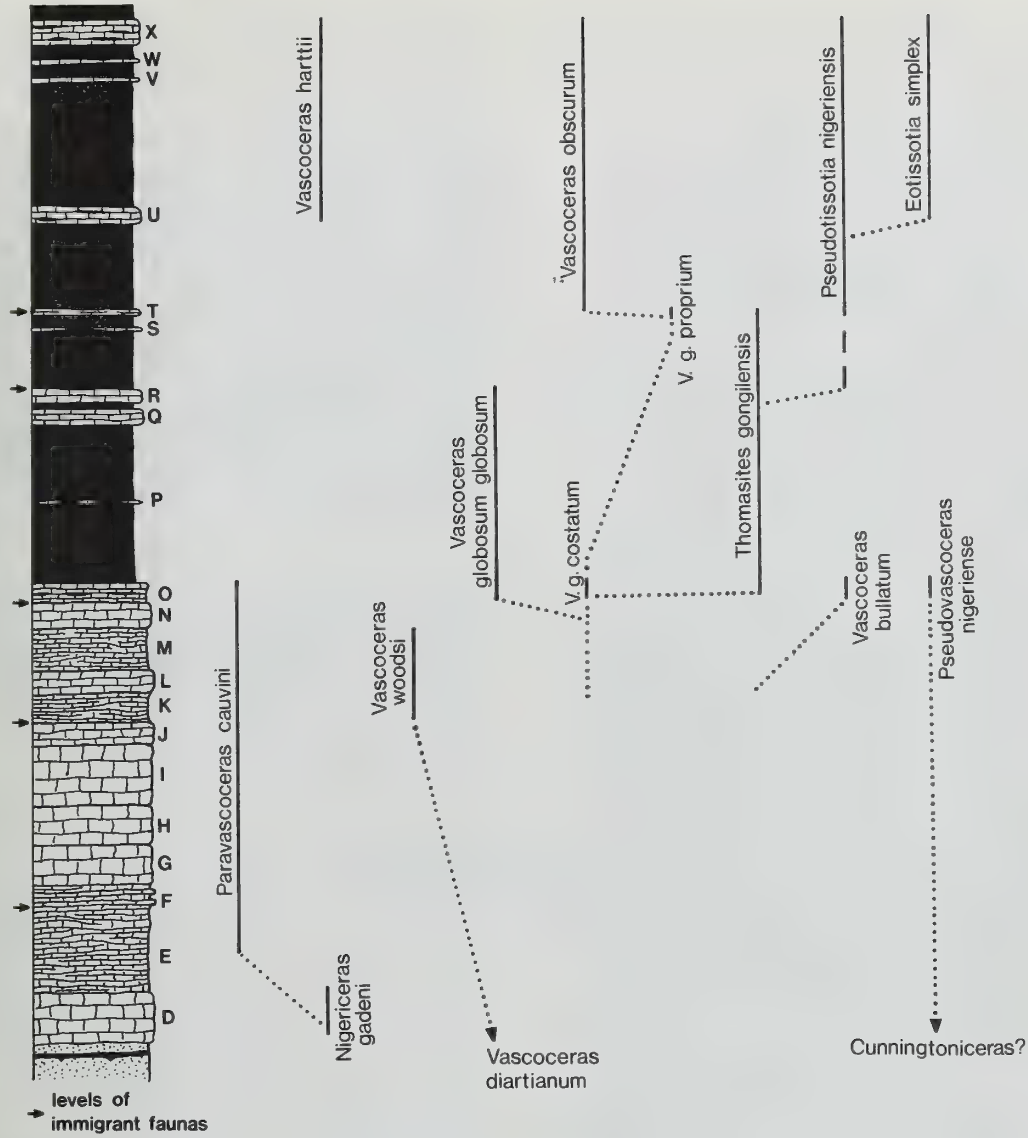

Fig. 65 Stratigraphical ranges in the Ashaka section of taxa mentioned in the text and their suggested phylogenetic relationships.

especially inter-regionally. A number of problems complicate their use including: the variable taxonomic treatment authors have employed; the difficulty of identifying poorly preserved material, especially if the inner whorls are not available; the lack of an exact stratigraphical provenance for many species; and the problem of polymorphism. In regard to the last of these factors Meister (1989) and Meister *et al.* (1992) have made the important point that in certain regions only a portion of the potential morphological range of a species may be expressed on account of palaeoecological factors.

It has long been appreciated that 'vascoceratid' ammonites are predominantly a Tethyan group. Less attention has been paid to the potential palaeoenvironmental influences on their regional distribution. In this regard it is of interest to compare the faunas of north-eastern Nigeria and Niger, the stratigraphical distributions of which are now well understood.

Despite their geographical proximity correlation between these two areas is not as straightforward as might be expected. There is little problem with the horizons of Geslinianum Zone age; in both places assemblages of *Nigericeras*, *Metoicoceras* and *Metengonoceras* are found. Similarly, in the upper part of the Turonian *Coilopoceras* is present in both areas. There are, however, faunal differences in the intervening sequences. *Vascoceras woodsi* is unknown in Niger. In Nigeria it occurs alongside *Pseudaspidoceras pseudonodosoides* which was compared with *P. tassaraense* Meister, Alzouma, Lang & Mathey (1992) from the Monts Iguelela area of Niger by Zaborski (1995). The two may be of comparable age. *P. tassaraense* occurs alongside *Nigericeras jacqueti involutum*, a form unknown in Nigeria. Slightly lower in the same section there occur large numbers of *Cibolaites*(?) *africaensis* Meister, Alzouma, Lang & Mathey (1992) which has not been found further to the south. At Tanout Aviation and Birgimari there are horizons dominated by compressed individuals of *Paravascoceras cauvini*. In their ornament or lack of it they match the variation shown by the species in unit O at Ashaka. The Niger faunas, however, include more inflated individuals of *Vascoceras crassum* type. None of the species associated with *P.*

cauvini in unit O at Ashaka is found in the described Niger horizons. Higher in the sequence *Thomasites gongilensis*, so abundant in unit R at Ashaka and unit O at Pindiga, and with an overall range from unit O to unit T2 at the former locality, is not found in any of the Niger sections. *Pseudotissotia nigeriensis*, on the other hand, occurs in large numbers at Tanout Aviation but none of the associated taxa in Nigeria accompany it there.

Biostratigraphical comparison between Niger and Nigeria is complicated by the fact that ammonites are restricted to limestone horizons which are, in the main, thin units within dominantly argillaceous sequences. The presence or absence of particular faunas, therefore, may in some cases be related to the occurrence of calcareous beds (see also Meister *et al.* 1992: 91). The possibility of control over ammonite distributions by transgressive pulses of the trans-Saharan sea during the Late Cenomanian and Early Turonian has long been discussed, most recently by Courville *et al.* (1991). Meister *et al.* (1992: 94–95), however, have speculated that local palaeoenvironments were a strong influence on 'vascoceratid' distributions, their morphological polymorphism and their consequent evolutionary potential. In support of the latter hypothesis it may be noted that members of evolutionary lineages 'indigenous' to north-eastern Nigeria (*Nigericeras*, *Paravascoceras cauvini* and *Pseudotissotia nigeriensis*) extend into Niger. Introduced taxa do not. Among these may be mentioned *Burroceras*? from unit F at Ashaka; *Vascoceras woodsi* from units K and M; the greater part of the fauna from unit O including *Pseudaspidoceras footeanum* (Stoliczka), *Fikaites*, *Rubroceras*, *Pseudovascoceras nigeriense* and, probably, *Vascoceras globosum costatum*; *Pseudaspidoceras paganum* from unit R; and *Pseudaspidoceras flexuosum*, *Watinoceras*, *Choffaticeras* and *Wrightoceras munieri* from unit T2. The appearances of these taxa are probably related to transgressive pulses, the influences of which did not fully extend into Niger. As suggested by Meister *et al.* (1992) the absence of these forms and consequent lack of competition may have permitted local intraspecific variants and evolutionary lineages to develop in Niger. Examples would be the inflated variants of *Paravascoceras cauvini* and the lineage leading to *Nigericeras jacqueti involutum*. Rather than the overall extent of the trans-Saharan sea as such, more localized influences such as water depth and temperature may have controlled the distribution of taxa. If these factors did apply they would place important constraints on the use of 'vascoceratid' species in long distance correlation.

Associated with the above matter is the probability that a number of acanthoceratine taxa independently gave rise to vascoceratid-like forms during Late Cenomanian times. Reyment (1979: 111) suggested that the family Vascoceratidae was polyphyletic, the morphological similarities between its members being due to adaptation to the same kind of epicontinental palaeoenvironments rather than to close phylogenetic affinities. The Late Cenomanian transgression brought several forms into north-eastern Nigeria which show elements of the 'vascoceratid' morphology, notably simplified sutures. *Rubroceras* and *Fikaites*, the latter probably derived from *Eucalycoceras* Spath, are examples, as is *Pseudovascoceras* which, as mentioned above, may be a descendent of *Cunningtoniceras*. Reyment (1955: 62, text-fig. 27) regarded *Nigericeras* as the root stock of the entire family Vascoceratidae while Cooper (1979) suggested that *Vascoceras diartianum* gave rise to both *Paravascoceras* and the younger *Vascoceras*. It is suggested here that *Paravascoceras* is derived from *Nigericeras* and belongs to a lineage separate to that leading to *Vascoceras*. The earliest *Vascoceras* in north-eastern Nigeria, *V. woodsi*, appears to be a peramorphic derivative of *V. diartianum*. The immediate origins of *V. bullatum*, *V. globosum* and *V. harttii* are obscure. It may be mentioned, however, that *V. globosum costatum* probably contains the progenitors of *Thomasites gongilensis*. This species in turn gave rise to *Pseudotissotia nigeriensis* in terminal Cenomanian times (see also Barber 1957, Cooper 1979, Meister 1989) from which *Eotissotia simplex* originated as a paedomorph during the Early Turonian (Zaborski 1993). The youngest member of the *V. globosum* group, *V. globosum proprium*, straddles the Cenomanian-Turonian boundary. It gave rise to *V. obscurum* and probably also *Neoptychites*. Kennedy & Wright (1979: 681) believed the latter genus to have been derived from *Paravascoceras* but used this name in the sense of *Vascoceras* without umbilical tubercles.

The suggested phylogenetic relationships of forms from north-eastern Nigeria are shown in Fig. 65. Several converging lineages are believed to exist, their frequently homeomorphic similarities being due to colonization of the same palaeoenvironment.

ACKNOWLEDGEMENTS. Thanks are due to Drs M. K. Howarth and H. G. Owen, and Mr. S. Baker for help in many ways. Dr. N. Morris kindly allowed access to a collection of ammonites from Niger. Mr. M. Baku, Quarry Manager, Ashaka Cement Co. kindly allowed easy access to the Ashaka quarry. Photographs were provided by the Natural History Museum (London) Photographic Unit. Dr. W. J. Kennedy kindly made useful suggestions concerning the manuscript.

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APPENDIX

A list of previously described material from Nigeria representing taxa discussed herein is given below with revised taxonomic determinations. The page and, where necessary, plate and figure numbers quoted are those in the original publications.

	Revised determination
Woods (1911)	
281 *Vascoceras nigeriense* sp. nov.	*Pseudovascoceras nigeriense* (Woods)
Reyment (1954*b*)	
256 *Vascoceras nigeriense* Woods	*Pseudovascoceras nigeriense* (Woods)
257 *Pachyvascoceras costatum* sp. nov.	*Vascoceras globosum costatum* (Reyment)
258 *Pachyvascoceras proprium* sp. nov.	*Vascoceras globosum proprium* (Reyment)
258 *Pachyvascoceras proprium plenum* subsp. nov.	*Vascoceras globosum proprium* (Reyment)
259 *Pachyvascoceras globosum* sp. nov.	*Vascoceras globosum globosum* (Reyment)
263 *Gombeoceras*? *bulbosum* sp. nov.	*Vascoceras globosum proprium* (Reyment)
Reyment (1955)	
63 *Paravascoceras* aff. *chevalieri* (Furon)	*Thomasites*
65 *Pachyvascoceras costatum* Reyment	*Vascoceras globosum costatum* (Reyment)
Barber (1957)	
15 *Vascoceras nigeriense* Woods	*Pseudovascoceras nigeriense* (Woods)
15 *Vascoceras robustum* sp. nov.	?*Vascoceras globosum costatum* (Reyment)
17 *Vascoceras polygonum* sp. nov.	?*Vascoceras globosum costatum* (Reyment)
17, pl. 4, fig. 1 *Vascoceras ellipticum* sp. nov.	?*Thomasites gongilensis* (Woods)
17, pl. 6, fig. 4 *Vascoceras ellipticum* sp. nov.	?*Vascoceras globosum proprium* (Reyment)
19 *Vascoceras bulbosum* (Reyment)	*Paravascoceras cauvini* (Chudeau)
19 *Vascoceras depressum* sp. nov.	*Paravascoceras cauvini* (Chudeau)
19 *Vascoceras obscurum* sp. nov.	*Vascoceras obscurum* (Barber)
21 *Vascoceras globosum globosum* (Reyment)	*Vascoceras globosum globosum* (Reyment) (part) and *V. globosum proprium* (Reyment) (part)
23 *Vascoceras globosum plenum* (Reyment)	*Vascoceras globosum proprium* (Reyment)
25 *Vascoceras globosum proprium* (Reyment)	*Vascoceras globosum proprium* (Reyment)
25 *Vascoceras globosum compressum* subsp. nov.	*Vascoceras globosum proprium* (Reyment)
25 *Vascoceras globosum carteri* subsp. nov.	*Vascoceras globosum globosum* (Reyment)
27 *Vascoceras* sp. juv.	*Vascoceras woodsi* sp. nov.
27 *Fagesia simplex* sp. nov.	indeterminate *Vascoceras*

27 *Fagesia involuta* sp. nov.	?*Vascoceras globosum globosum* (Reyment)
29 *Nigericeras costatum* sp. nov.	*Pseudovascoceras nigeriense* (Woods)
29 *Nigericeras glabrum* sp. nov.	*Pseudovascoceras nigeriense* (Woods)
31 *Nigericeras*(?) *intermedium* sp. nov.	*Pseudovascoceras nigeriense* (Woods)
31 *Paramammites tuberculatus* sp. nov.	*Pseudovascoceras nigeriense* (Woods)
33 *Paramammites raricostatus* sp. nov.	*Pseudovascoceras nigeriense* (Woods)
33 *Paramammites inflatus* sp. nov.	*Pseudovascoceras nigeriense* (Woods)
35 *Paravascoceras costatum costatum* (Reyment)	*Vascoceras globosum costatum* (Reyment)
35 *Paravascoceras costatum quadratum* subsp. nov.	*Vascoceras globosum costatum* (Reyment)
37 *Paravascoceras costatum tectiforme* subsp. nov.	*Vascoceras globosum costatum* (Reyment)
37 *Paravascoceras* aff. *cauvini* (Chudeau)	?*Paravascoceras cauvini* (Chudeau)
Meister (1989)	
10 *Nigericeras gadeni* (Chudeau) – *lamberti* Schneegans	*Paravascoceras cauvini* (Chudeau)
11 *Nigericeras jacqueti* Schneegans	*Paravascoceras cauvini* (Chudeau)
11 *Plesiovascoceras* aff. gr. *thomi* (Reeside) ou sp. nov.	*Vascoceras woodsi* sp. nov.
12 *Neoptychites cephalotus* (Courtiller)	*Thomasites*
14, pl. 5, fig. 2 *Paravascoceras* gr. *evolutum* Schneegans	?*Pseudaspidoceras pseudonodosoides* (Choffat)
14, pl. 5, fig. 4 *Paravascoceras* gr. *evolutum* Schneegans	*Vascoceras woodsi* sp. nov.
14 *Paravascoceras nigeriensis*(?) (Woods)	*Pseudovascoceras nigeriense* (Woods)
14 *Paravascoceras* aff. *nigeriensis* (?) (Woods)	*Paravascoceras cauvini* (Chudeau)
18 *Paravascoceras crassum* Furon	*Vascoceras bullatum* Schneegans
21 *Paravascoceras tectiforme* (Barber)	*Vascoceras globosum costatum* (Reyment)
21, pl. 9, fig.1 *Paravascoceras carteri* Barber	*Vascoceras bullatum* Schneegans
21, pl. 10, figs 1, 2 *Paravascoceras carteri* Barber	*Vascoceras globosum globosum* (Reyment)
23 *Vascoceras costatum* (Barber)	*Pseudovascoceras nigeriense* (Woods)
23 *Vascoceras costatum* (Barber) *glabrum* (Barber)	*Pseudovascoceras nigeriense* (Woods)
28 *Vascoceras ellipticum Barber*	*Pseudovascoceras nigeriense* (Woods)
28 *Vascoceras silvanense* Choffat	indeterminate *Vascoceras*
28 *Vascoceras obscurum* Barber	*Vascoceras obscurum* Barber
30 *Paramammites subconciliatus* (Choffat)	*Pseudovascoceras nigeriense* (Woods)
36, pl. 14, figs 3, 4 *Paramammites polymorphus* (Pervinquière)	*Pseudovascoceras nigeriense* (Woods)
36, pl. 15, figs 2, 3 *Paramammites* aff. gr. *polymorphus* (Pervinquière)	*Fikaites varicostatus* Zaborski
37 *Fagesia superstes* var. *levis* Renz	*Vascoceras harttii* (Hyatt)
Pl. 16, fig. 1 *Thomasites*?	*Fikaites varicostatus* Zaborski
Zaborski (1990a)	
Figs 8, 12–15 *Vascoceras cauvini* Chudeau	*Paravascoceras cauvini* (Chudeau)
Figs 9, 10 *Vascoceras* sp.	*Vascoceras woodsi* sp. nov.
Fig. 11 *Vascoceras bulbosum* (Reyment)	*Paravascoceras cauvini* (Chudeau)
Figs 16–18, 20, 21 *Vascoceras* sp. juv.	*Vascoceras woodsi* sp. nov.
Fig. 25 *Vascoceras nigeriense* Woods	*Pseudovascoceras nigeriense* (Woods)
Courville (1992)	
Pl. 4, figs 1–3 *Vascoceras* gr. *cauvini* Chudeau	*Paravascoceras cauvini* (Chudeau)
Pl. 5, fig. 1 *Vascoceras* gr. *thomi* (Reeside) ou *evolutum* (Schneegans)	*Vascoceras woodsi* sp. nov.
Pl. 5, fig. 2 *Vascoceras* gr. *crassum* (Furon) ou *costellatum* Collignon	*Vascoceras bullatum* Schneegans
Pl. 5, fig. 3; pl. 6, figs 2, 3 *Vascoceras* sp. gr. *costatum* (Barber)	*Pseudovascoceras nigeriense* (Woods)
Pl. 7, figs 1, 2 *Vascoceras tectiforme* (Barber)	*Vascoceras globosum costatum* (Reyment)
Pl. 7, fig. 3 *Vascoceras tectiforme* (Barber)	*Vascoceras globosum globosum* (Reyment)
Pl. 8, figs 1, 2 *Vascoceras* gr. *globosum* (Reyment) ou *Fagesia* sp.	*Vascoceras globosum globosum* (Reyment)
Pl. 9, fig. 1 *Vascoceras* gr. *globosum* (Reyment) ou *Fagesia* sp.	*Vascoceras harttii* (Hyatt)
Pl. 10, fig. 1 *Vascoceras* sp?	?*Fikaites varicostatus* Zaborski
Pl. 10, figs 2, 3 *Vascoceras* sp. aff. *obscurum* Barber	*Vascoceras globosum proprium* (Reyment)